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MORPHOLOGY, PALEOECOLOGY, AND PHYLOGENY
OF THE PERMO-PENNSYLVANIAN AMPHIBIAN
DIPLOCERASPIS

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No. 2 *Morphology, Palaeoecology, and Phylogeny of the
Permo-Pennsylvanian Amphibian DIPLOCERASPIS*¹

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INTRODUCTION

The Permo-Carboniferous lepospondylous amphibian, *Diplocaulus*, has long attracted paleontological interest because of the remarkable horn-like extensions of the posterior lateral corners of the skull. Several earlier Carboniferous (Westphalian) amphibians, *Keraterpeton*, *Batrachiderpeton*, and *Diceratosaurus*, possess "horns," though very much shorter ones, and have been thought to include the ancestry of *Diplocaulus*. In 1952 A. S. Romer described, from the Permo-Carboniferous of the Appalachian region, an amphibian which bears "long horns" similar to those of *Diplocaulus*. Although the amount of material was small and the skulls were fragmentary, it sufficed to distinguish a new genus, *Diploceraspis*. Romer suggested that this amphibian represented an evolutionary lineage paralleling *Diplocaulus* in adaptation, and was derived from a different Westphalian "horned" type than the latter. Because of similarly sculptured neural arches he tentatively related *Diploceraspis* to the "short-horned" *Diceratosaurus*.

Douthitt (1917) devoted a monograph to *Diplocaulus* and to interpretation of that unusually adapted skull. Whatever selective factors directed the evolution of this adaptation, similar ones must have acted on the *Diploceraspis* lineage. A comparative study of both genera elucidates the adaptation and assists in clarifying the phyletic relation of both to more primitive, "short-horned" types. Unfortunately, the specimens available to Romer were inadequate for such a study. During the summers of 1954-57, however, field parties from Lafayette College collected a large quantity of *Diploceraspis* material. Availability of these specimens permits a much more detailed and complete description of *Diploceraspis* and a more thorough comparison with *Diplocaulus* and with the possible ancestral types from Westphalian rocks.

ACKNOWLEDGMENTS

Grants from the Society of Sigma Xi, the American Academy of Arts and Sciences, the Geological Society of America, and the National Science Foundation (N.S.F. G 2156) supported the field work and provided assistance in the preparation of the fossils. Study of the *Diploceraspis* material and preparation of portions of this paper were undertaken during sabbatical leave granted by Lafayette College.

Dr. Herbert Barghusen served as field assistant and was responsible for the discovery of locality 7-55 which yielded the

greater portion of the *Diploceraspis* specimens, including a complete skull. Mr. Wilson Piatt conducted most of the preparation as an undergraduate research assistant.

Dr. Donald Baird loaned me a series of latex casts of *Diceratosaurus* and *Ptyonius* specimens from the Westphalian vertebrate locality at Linton, Ohio. I should like, also, to acknowledge the courtesy of the staff of the American Museum of Natural History (AMNH), of the Museum of Comparative Zoology (MCZ), and of the Carnegie Museum (CM) in making specimens of *Diplocaulus* and *Diploceraspis* available for comparative study.

THE MATERIALS AND THEIR STRATIGRAPHIC OCCURRENCE

The original *Diploceraspis* specimens described by Romer (1952) were collected by parties from Carnegie Museum (Burke, 1935). Most of these came from localities within the Dunkard group (very late Stephanian or early Autunian), but a few were found in a Conemaugh (early Stephanian) locality. Romer placed all the Dunkard *Diploceraspis* in a single species, *D. burkei*, but separated the Conemaugh *Diploceraspis* as *D. conemaughensis* (see discussion below). The Carnegie collections include vertebrae, a clavicle, other fragmentary clavicular or interclavicular specimens, several incomplete skulls, and several "horns" and other fragmentary skull material.

The new material, described in some detail below, includes several hundred vertebrae, numerous complete as well as fragmentary clavicles, several interclavicles, some ribs and limb fragments that may belong to *Diploceraspis*, a hundred or more "horn" fragments, several partial lower jaws, several incomplete skulls of various sizes, and a single nearly perfect skull. No articulated skeletal material has yet been found. All specimens occurred in limestone and/or in limy shale intimately associated with limestone. Table 1 gives a list of Dunkard *Diploceraspis* localities and a summary of specimens from each. Nearly all *Diploceraspis* localities, old and new, occur near the center of the northern portion of the Dunkard basin — southern Marshall and northern Wetzel counties in West Virginia, southwestern Greene County in Pennsylvania, and northeastern Monroe County in Ohio. A second, small concentration appears in the center of the southern portion of the basin — Wood County, West Virginia. Of the thirty-one *Diploceraspis* localities, one occurs in the upper part of the Conemaugh group; two in the lower part of the Washington Formation, the basal unit of the Dunkard group; three

TABLE 1. SUMMARY OF *DIPLOCERASPI*S LOCALITIES

Locality-Carnegie (Moran 1952)	Material	Location	Stratigraphic Position
1	Vertebrae and skull fragments of <i>D. conemaughensis</i>	Soho St. Quarry, Pittsburgh, Penna.	Conemaugh gr. Forty feet below Pittsburgh coal
6	Vertebra	Adams Township, Monroe Co., Ohio	Lower Washington Fm.
7	Skull fragments	Sand Hill Dist., Marshall Co., W. Va.	Lower Washington Fm.
13	Vertebrae	Proctor Dist., Wetzel Co., W. Va.	Lower Greene Fm.
14	Vertebra, clavicle	Liberty Dist., Marshall Co., W. Va.	Lower Greene Fm.
16	Clavicle	Tucker Dist., Wirt Co., W. Va.	Middle Greene Fm.
18	? Vertebrae	Clay Dist., Marshall Co., W. Va.	Middle Greene Fm.
20	Clavicle, vertebrae	Clay Dist., Marshall Co., W. Va.	Middle Greene Fm.
21	? Vertebrae	Liberty Dist., Marshall Co., W. Va.	Middle Greene Fm.
23	? Vertebrae	Proctor Dist., Wetzel Co., W. Va.	Middle Greene Fm.
24	? Vertebrae	Springhill Township, Greene Co., Penna.	Middle Greene Fm.
26	Partial skulls, vertebrae	Liberty Dist., Marshall Co., W. Va.	Upper Greene Fm.
27	Vertebrae	Meade Dist., Marshall Co., W. Va.	Upper Greene Fm.
28	Vertebrae	Battelle Dist., Monongalia Co., W. Va.	Upper Greene Fm.

Locality- Carnegie (Moran 1952)	Material	Location	Stratigraphic Position
29	? Vertebrae	Franklin Dist., Marshall Co., W. Va.	Upper Greene Fm.
30	? Vertebrae	Franklin Dist., Marshall Co., W. Va.	Upper Greene Fm.
L	Vertebrae	Tucker Dist., Wirt Co., W. Va.	Upper Greene Fm.
35	Skull fragments, vertebra	Proctor Dist., Wetzel Co., W. Va.	Upper Greene Fm.
36	Skull fragments (horns)	Center Dist., Wetzel Co., W. Va.	Upper Greene Fm.
37	Vertebra	Proctor Dist., Wetzel Co., W. Va.	Upper Greene Fm.
Locality- Lafayette			
5-55	Vertebra, clavicle	Limestone, elevation 1360', 0.5 mi. E. of intersection of W. Va. 89 and U.S. 250 in cut on W. Va. Rt. 89, 80°32' 37"W, 39°52' 15"N	Middle Greene Fm.
6-55	Skull and mandible fragments, vertebrae, clavicles and inter- clavicles	Lime sandstone and congl., elevation 1352', 0.2-0.3 mi. N of north boundary of Sherrard on W. Va. Rt. 88, Union Dist., Marshall Co., 80°40' 57"W, 39°59' 34"N	Middle Greene Fm.
7-55	Complete skull, partial skulls, skull fragments, partial mandibles, vertebrae, ribs, clavicles, inter- clavicles.	Limestone, elevation 1282', 1.5 mi. N of north boundary of Sherrard on W. Va. Rt. 88 Union Dist., Marshall Co., 80°41' 35"W, 40°0' 22"N	Middle Greene Fm.

TABLE 1. SUMMARY OF *DIPLOCEASPIIS* LOCALITIES (Cont.)

Locality-Lafayette	Material	Location	Stratigraphic Position
9-55	Vertebrae	Limestone, elevation 1060', 0.7 mi. E of Bristonia on Holbrook Road, 80°23' 23" N, 39°51' 52" N, Richhill Township, Greene Co., Penna.	Lower Greene Fm.
13-55	Vertebra, clavicle	Locality 28 of Moran. Corrected elevation 1385', 80° 24" W, 39°39' 36" N, Battelle Dist., Monongalia Co., W. Va.	Upper Greene Fm.
15-55	Vertebrae	Limestone and limy shale, elevation 1330, ridge crest west of Uniontown on W. Va. Rt. 7, 80°34'23"W, 39°38' N, Center Dist., Wetzel Co., W. Va.	Upper Greene Fm.
17-55	Partial skull	Limestone and limy shale, elevation 1240', on east side of hill east of Knob Fork, W. Va. Rt. 7, 80°31' 52"W, 39°38' 47"N, Center Dist., Wetzel Co., W. Va.	Middle Greene Fm.
18-55	Skull fragments, vertebrae	Limestone, elevation 1085', road running SE to Wayne Ridge from W. Va. Rt. 2 just north of Kent, 80°50' 40"W, 39°46' 25"N, Franklin Dist., Marshall Co., W. Va.	Middle Greene Fm.

Locality-	Material	Location	Stratigraphic Position
Lafayette 21-55	Vertebrae	Limestone and limy shale, elevation 1195', Great House Hill Road north of W. Va. Rt. 7, 1/2 mi. east of Wileysville, 80°38'57"W, 39°37'23"N, Center Dist., Wetzel Co., W. Va.	Upper Greene Fm.
22-55	Skull fragments, partial mandibles, vertebrae, interclavicles, clavicles	Limestone and shaley ls., elevation 1050', Brock Ridge Road north of W. Va. Rt. 7, about 1 mi. west of Wileysville, 80°42'7"W, 39°37'30"N, Proctor Dist., Wetzel Co., W. Va.	Middle Greene Fm.
1-56	Vertebrae	Limestone and limy shale, elevation 960', 2.0-1.75 mi. west of Murphytown on U.S. Rt. 50, 81°27'40"W, 39°14'30"N to 81°28'30"W, 39°14'45"N, Clay Dist., Wood Co., W. Va.	Middle Greene Fm.
2-56	Skull fragments, vertebrae, clavicle	Limestone, elevation 960', Montgomery Hill east of Murphytown on U.S. Rt. 50, 81°24'50"W, 39°14'40"N, Clay Dist., Wood Co., W. Va.	Middle Greene Fm.
4-56	Skull fragment (horn)	Limestone, elevation 1060', Limestone Hill on Gates Road 0.4 mi. west of U.S. 21 (Probably Moran's localities L and 31), 81°32'20"W, 39°2'53"N, Steele Dist., Wood Co., W. Va.	Upper Greene Fm.

in the lower part of the Greene Formation, the upper unit of the Dunkard group; fourteen in the middle Greene; and eleven in the upper Greene. The upper Conemaugh is generally regarded as mid-Stephanian (early Virgilian) age. The Dunkard may bridge the Stephanian-Autunian boundary; the vertebrates of the middle Greene suggest early Autunian. A complete discussion of Dunkard stratigraphy and vertebrate occurrences will be published separately.

MORPHOLOGY

INTRODUCTION

Diploceraspis, quite plainly, is a lepospondyl and, just as clearly, belongs to the order Nectridea. Romer (1945) recognized three families: Lepterpontidae, Urocordylidae, and Keraterpetontidae. The latter group includes a poorly understood form, *Scincosaurus*, the three "short-horned" forms, *Diceratosaurus*, *Keraterpeton*, and *Batrachiderpeton*, and the "long-horned" *Diplocaulus* (Figs. 12, 13). *Diploceraspis* appears to belong to this group, and comparisons here emphasize these genera but refer to the urocordylids as well.

Diceratosaurus was most completely described by Jaekel (1903) with later notes by Moodie (1916) and Romer (1930); Watson (1913) described *Batrachiderpeton*; Steen (1938) restudied *Urocordylus*, *Scincosaurus*, and *Keraterpeton*; and Douthitt (1917) gave the most complete discussion of *Diplocaulus*. Olson (1951) analysed relative growth in *Diplocaulus*. In addition to this published work, I have examined the *Diceratosaurus* material displayed in a superb series of casts prepared by Dr. Donald Baird, Princeton University, and also studied the *Diplocaulus* skulls in the collection of the American Museum of Natural History.

SKULL

General form. The observer's initial impression of a *Diploceraspis* skull (Figs. 1, 2, 3) is of a flattened, short-faced form, like that of *Diceratosaurus* or *Keraterpeton*, on to which have been grafted two flat "horns," albeit unusually slender ones, from a *Diplocaulus*. In *Diplocaulus* the line of horn and face forms a broad, continuous curve or, in other terms, the face is wide so that the horns and face form a single, crescentic unit. In *Diploceraspis*, on the contrary, the line of horn is quite straight,

and it meets the curved line of the face with a relatively sharp break (a concave curve) at the posterior end of the orbits. The *Diploceraspis* face, therefore, is relatively long and narrow compared to that of *Diplocaulus* (Fig. 13).

The fragmentary condition of most skull material makes precise size comparisons difficult. Specimen MCZ 3009, the complete *D. burkei* skull, is 55.7 mm. long, from snout tip to occipital border along the midline, and appears to be the largest *Diploceraspis* in the collections (Table 2). This is about half the length of a large *Diplocaulus*. The smallest *D. burkei* skull is represented by a fragmentary jugal, MCZ 3015, which is about one-third the breadth of the similar element in MCZ 3009. A still smaller skull (CM 8544), with a jugal about half the width of that in MCZ 3015, was assigned by Romer to *D. conemaughensis*. Other *D. conemaughensis* appear to overlap *D. burkei* in size.

As indicated, the horns appear narrower and straighter than those in *Diplocaulus*, but it is very difficult to measure this apparent difference because of the lack of any inflection between face and horn in the latter genus. The horns taper evenly and gradually toward the tips — in some individuals (MCZ 3032) the taper is so very gradual that the distal end of the horn is extremely long and narrow (Fig. 6). In some this portion is gently curved. The horn tips are recurved posteromedially to a varying degree and are serrate along their anterolateral edges. The internal space within the horn constricts distally so that near the tips the horns are, for practical purposes, solid bone. The horn tips were subject to abnormal growth, since in specimen MCZ 3009 (Fig. 6) the right horn tip recurves anterolaterally rather than posteromedially.

The small skull, CM 8551, described and illustrated by Romer (1952), shows a much greater angle between horns than the two new ones, MCZ 3009 and MCZ 3012, which also show both sides of the skull. MCZ 3009 is approximately 75 per cent larger than CM 8551, MCZ 3012 30 per cent larger. Three fragmentary specimens, MCZ 3013, MCZ 3010, and MCZ 3019, the first about 50 per cent smaller than CM 8551, the second about the same size, and the third about 30 per cent larger, show intermediate angles. A postparietal, about the same size as that of MCZ 3009, indicates a similar horn angle. The angle, therefore, shows individual variation but seems to decrease with size, in contrast to *Diplocaulus* in which it increases (Olson, 1951). When size is considered, the angle between the horns is rather small — distinctly less so than in *Diplocaulus magnicornis* and about the same as in *Diplocaulus*

TABLE 2A
DIMENSIONS OF *DIPLOCERASPIS* SPECIMENS

Explanation of measurements. Based on Olson's study of *Diplocaulus* (1951). Measurements not used by Olson are starred.

- Sk₁ = Distance from tip of snout at premaxillary suture to posterior margin at postparietal suture.
- Sk_{w1} = Distance between posterolateral corner of tabulars.
- Sk_{w2} = Distance between lateral ends of occipital condyles.
- Pi-Fr = Distance from anterior margin of pineal opening to frontal-parietal suture at junction of suture between parietals.
- I_{p1} = Distance from anterior termination of suture between postparietals at point of intersection of more posterior postparietal-parietal suture to posterior termination of the suture between the postparietals.
- Pa₁ = Distance along suture between parietals from frontal suture to anterior parietal-postparietal suture.
- Fr₁ = Length of frontal along midline.
- O-S₁ = Distance along midline from anterior edge of orbits to snout tip.
- Io_w = Minimum distance between orbits.
- *Eo_w = Maximum distance between lateral margins of orbits.
- O_w = Greatest orbital width perpendicular to midline.
- O_l = Greatest orbital length parallel to midline.
- Pmx₁ = Distance from posterior termination of suture between premaxillae to intersection of this suture with tip of snout.
- Nar_w = Distance between medial borders of nares.
- Po₁ = Distance from midpoint of postfrontal-postorbital suture to posterior corner of postorbital.
- Pa_w = Distance perpendicular to midline from suture between parietals to junction of parietal, squamosal, and tabular.
- Ip_w = Distance perpendicular to midline from posterior termination of suture between parietals to greatest lateral extent of postparietal.
- Sq_w = Distance from midline of skull to lateral point of squamosal.
- *J_w = Distance from midline of skull to lateral point of jugal.
- St₁ = Distance from junction of parietal, postparietal, and tabular to tip of horn.
- *H_w = Distance from posterior termination of suture between postparietals to posterolateral corner of quadratojugal.
- *Sq_b = Greatest width of squamosal on ventral surface, perpendicular to lateral border of horn.
- *T₁ = Length from tip of horn to lateral end of otic notch.
- *Ot₁ = Distance from lateral end of pterygoid-exoccipital suture to lateral end of otic notch.
- *Ot_w = Width across otic notch from posterolateral end of quadratojugal-squamosal suture to opisthotic, perpendicular to posterior border of horn.
- *C₁ = Length of centrum on ventral midline.
- *C_w = Width of centrum across posterior face.

*V_h = Height of vertebra from ventral points of centrum to top of neural spine.

*NS_h = Height of neural spine above level of zygapophyses.

*Tr_w = Width between tips of transverse processes.

*HS_d = Distance from posteroventral edge of centrum to ventral edge of haemal arch.

TABLE 2B

DIMENSIONS OF *DIPLOCERASPIS* SPECIMENS

Tabulation of measured skulls. See Table 2A for explanation of measurements.

Dimensions in millimeters.

	MCZ 3009	CM 8548	MCZ 3010	MCZ 3013	MCZ 3018	MCZ 3019	MCZ 3012
Sk ₁	55.7						
Skw ₁	191.8	116 ±					117.0
Skw ₂	20.0		14.2?				
Pi-Fr	5.7						
I _{p1}	11.9			6.0	5.8		
Pa ₁	13.1						
Fr ₁	21.0	17.0					
O-S ₁	11.8	9.0					
Io _w	11.2	8.5 ±					
Eo _w	30.0						
O _w	8.4						
O ₁	11.8						
Pmx ₁	8.0						
Nar _w	11.5	10.0 ±					
Po ₁	7.2						
Pa _w	37.3			19.7	23.7 ±		
Ip _w	36.8			22.6	31.3 ±	28.4	
Sq _w	70.2			39.7			
J _w	25.0			17.3			
St ₁	84.9						
H _w	36.8			23.9			

SPECIMEN	Sq _b	T ₁	Ot ₁	Ot _w
MCZ 3009	13.9	83.7	32.7	17.8
CM 8544	3.2	11.2 ±	8.2 ±	6.6 ±
MCZ 3032		90?		
MCZ 3010	8.3	48.6	19.8 ±	17.5 ±
MCZ 3026	8.1			
MCZ 3013	6.8	28.5	17.4	10.7
MCZ 3016	7.0 ±			

TABLE 2B (Cont.)

SPECIMEN	Sq _b	T ₁	Ot ₁	Ot _w
MCZ 3033	7.9 6.1 5.3 8.0 8.4 4.0			
MCZ 3018	8.3		17.5	
MCZ 3017	7.5 ± 7.1	71.6 49.5 ± 51.4		
MCZ 3019			19.0	13.0 ±
MCZ 3012		53.0 ±		

TABLE 2C
DIMENSIONS OF *DIPLOCERASPIS* SPECIMENS

Tabulation of measured vertebrae. See Table 2A for explanation of measurements. Dimensions in millimeters.

Specimen	Region	C ₁	C _w	V _h	NS _h	Tr _w	HS _d
MCZ 3020	"Atlas"	5.0	3.2	—	—	7.9	—
		6.0	4.0	8.7	5.2	9.0	—
		5.6	3.5	—	—	8.2	—
		5.6	—	8.3	5.3	8.7	—
		5.5	3.8	—	—	8.8	—
MCZ 3029	"Atlas"	—	—	—	—	9.4	—
		5.7	3.8	—	—	9.4	—
MCZ 3030	"Axis"	5.2	4.1	7.8	5.0	10.4	—
MCZ 3024	"Axis"	4.9	3.2	7.7	4.6	—	—
		5.9	3.4	7.8	4.8	8.0 ±	—
		3.2	1.9	5.5	3.1	—	—
		6.0	3.9	9.4	5.7	9.2	—
MCZ 3003	"Dorsal"	8.5	3.4	7.7	4.0	10.4	—
MCZ 3027	"Dorsal"	9.1	4.5	—	—	11.4	—
		7.7	4.9	9.3	5.0	—	—
		8.5	4.3	—	—	13.2	—
		7.5	3.8	8.7	4.7	—	—
		8.7	3.4	7.8	—	—	—
		10.9	—	—	—	—	—
		8.5	3.0	8.3	4.0	—	—
		9.0	3.0	8.7	4.6	—	—
		10.3	—	7.9	4.6	—	—
		9.1	—	8.4	3.7	—	—
		7.8	3.0	6.9	3.9	—	—
7.3	—	6.8	—	—	—		
8.4	—	8.8	3.3	—	—		

TABLE 2C (Cont.)

Specimen	Region	C ₁	C _w	V _h	NS _h	Tr _w	HS _d		
MCZ 3005	"Dorsal"	12.0 ±	—	—	—	13.2	—		
		10.0	—	8.9	—	—	—		
MCZ 3023	"Dorsal"	10.0	4.8	9.8	4.7	14.0 ±	—		
		10.0	4.0	9.5	4.5	—	—		
		12.1	—	—	—	—	—		
		11.2	4.1	9.4	—	14.2	—		
		9.5	3.8	9.3	4.8	—	—		
		7.6	3.8	8.9	5.3	—	—		
		8.7	3.2	8.1	4.0	—	—		
		9.4	3.9	7.3	3.5	8.9	—		
		9.5	—	8.8	4.3	—	—		
		10.7	5.7	12.4	6.7	14.0 ±	—		
		13.3	5.0	12.1	6.2	—	—		
		5.0	2.9	—	—	—	—		
		MCZ 3033	"Dorsal"	6.6	3.1	8.4	4.7	—	—
				11.4	4.3	9.3	4.0	—	—
8.0	—			8.2	—	—	—		
9.7	3.8			9.1	4.2	10.7	—		
9.1	4.7			10.5	5.6	13.6	—		
8.4	3.6			8.9	4.5	—	—		
7.3	—			7.8	—	—	—		
5.2	2.3			5.8	—	—	—		
8.0	3.5			8.9	3.6	8.4	—		
8.5	3.4			9.0	4.3	10.2	—		
8.9	4.0			9.4	4.5	—	—		
9.4	4.1			9.8	5.0	—	—		
8.2	3.4			6.1	—	10.1	—		
8.9	3.7			9.1	5.0	13.6	—		
6.9	2.9			8.6	5.0	8.8	—		
5.9	3.7			7.8	3.9	10.6	—		
5.7	1.7			4.1	1.7	—	—		
9.9	3.2	7.7	—	—	—				
8.0	2.9	6.9	3.4	—	—				
MCZ 3006	"Sacral"	8.8	3.2	7.0	—	—	8.7		
MCZ 3007	"Caudal"	12.5	3.3	8.2	3.8	—	13.4		
MCZ 3021	"Sacral"	9.9	3.4	6.4	3.5	—	10.7		
	"Sacral"	8.0	2.5	4.8	2.0	—	8.0		
	Ant.								
	Caudal ?	8.2	1.9	4.8	2.6	—	8.0		
MCZ 3008	Ant.								
	Caudal ?	2.3	—	1.07	—	—	2.4		
MCZ 3028	Caudal	9.0	—	5.8	—	—	9.6		
		9.3	1.4	4.3	1.7	—	6.4		
		10.4	—	6.3	2.6	—	10.2		

TABLE 2C (Cont.)

Specimen	Region	C ₁	C _w	V _h	NS _h	Tr _w	HS _d
MCZ 3032	Caudal	13.9	3.8	7.7	—	—	13.8
		11.0	3.8	7.4	—	—	12.7
		9.2	2.2	4.8	2.1	—	7.7
		9.2	1.9	5.1	2.1	—	7.8
		10.2	2.3	4.4	1.5	—	7.3

brevirostris (Fig. 13). Since *Diplocaulus* horns are curved backward, the angle decreases distally. In consequence, *Diploceraspis* horns angulate more sharply proximally than those of *Diplocaulus brevirostris* but less so distally. The posteromedial border of the horn is inflected anteriorly near the midline before it turns medially to the nearly straight, transverse, occipital border. In consequence, the posterior edge of the postparietal displays a very flat S-curve, convex backward distally, concave backward proximally. The acuity of these curves varies from individual to individual.

The position and character of orbits and external nares reflect the length and the narrowness of the *Diploceraspis* face. The ratio of the interorbital width to the breadth of skull at the anterior end of orbits is 0.39 in *Diploceraspis*, as compared with 0.19 in *Diplocaulus*, and the orbits are elongated anteroposteriorly as compared with *Diplocaulus*. The nares open on the anteroventral border of the skull as in *Diplocaulus*, but extend further upward and backward onto the dorsal surface.

As described by Romer, the skull surface is sculptured by small pits, differing from those of *Diplocaulus* only in size. These pits are roughly circular, although those adjacent to some of the sutures are elongated parallel to the suture line. In a very small specimen of *Diploceraspis burkei* (MCZ 3015, a fragmentary squamosal) they range from 0.2 to 0.3 mm. in diameter. On the squamosal of the larger specimen, MCZ 3013, they average about 0.4 mm., and on the squamosal of the still larger one, MCZ 3009, about 0.6-0.7 mm. In the smallest *Diploceraspis conemaughensis*, CM 8544, the pits are approximately 0.1 mm. in diameter. This specimen is about half the size of MCZ 3015. In other *D. conemaughensis*, they are similar in size to those of comparable *D. burkei* specimens. The lateral line system is described in a subsequent paragraph.

The palatal aspect of the skull is generally similar to that of *Diplocaulus*. The quadrate articulates with the lower jaw far forward — approximately on a line with the posterior border of

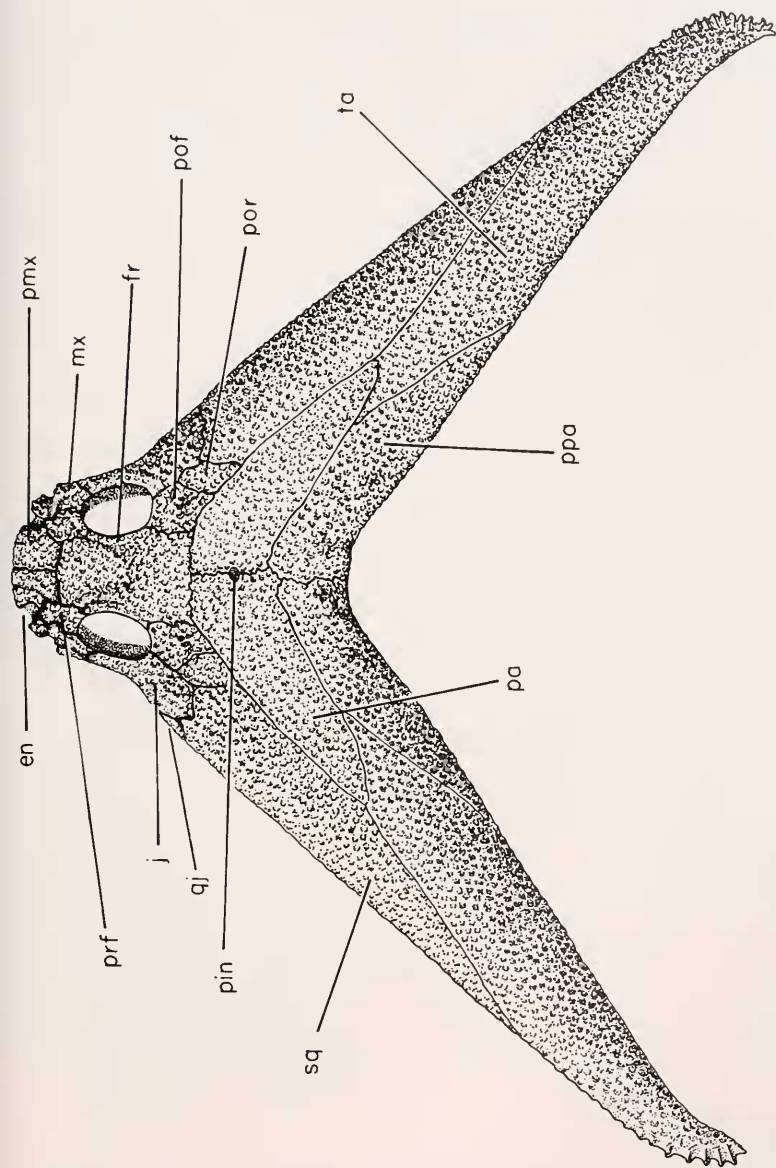


FIG. 1. *Diplocoeraspis* skull, reconstructed dorsal view. Approximate enlargement, x 0.8. Abbreviations: *en*, external naris; *fr*, frontal; *j*, jugal; *mx*, maxilla; *pa*, parietal; *pin*, pineal; *pmx*, premaxilla; *pof*, postfrontal; *por*, postorbital; *ppa*, postparietal; *prf*, prefrontal; *qj*, quadratojugal; *sq*, squamosal; *ta*, tabular.

the frontal, midway between the occipital condyles and the front of the skull. The interpterygoid vacuities are very large; the subtemporal fossae are relatively small but extend posteriad a considerable distance (Fig. 4). The otic notches, like those of *Diplocaulus*, have rotated completely onto the ventral surface and form elongate, ellipsoidal openings under the proximal portion of each horn. The internal nares are surrounded almost completely by the vomers and palatines; the maxilla and premaxilla are nearly excluded from the narial border. The ventrolateral border of the skull turns sharply upward in front of the quadrate so that the depth of the skull at the front end of the quadratojugal is about twice that at the anterior end of the jugal. In consequence, the ventral border of the lower jaw lies in line with the ventral border of the quadratojugal, and the jaw is approximately as deep as the facial region of the skull. *Diploceraspis* lacks the ventral flange of the quadratojugal which in *Diplocaulus* extends markedly below the ventral surface of the horn.

Corresponding to the relative narrowness of the *Diploceraspis* face, the arch of marginal and palatal teeth is narrow rather than broadly rounded as it is in *Diplocaulus*. The row of vomerine teeth lies immediately posterior to the premaxillary teeth and, therefore, in front of the anterior margin of internal nares rather than behind as in *Diplocaulus*. The tooth row is relatively short, even more so than that of *Diplocaulus*. The marginal row comprises 14 or 15 teeth on each side and terminates along a transverse line just behind the posterior border of the internal nares. The palatal row extends somewhat more posteriad, to a point near the posterior border of the orbits, and consists of 17 or 18 teeth on each side. The arch of the lower jaw is correspondingly short and narrow and includes 11 teeth on either side. The teeth, both marginal and palatal, are sharply to squatly conical; the tips are invariably sharp and, on a few teeth, are slightly recurved. A few, two or three, coronoid teeth, similar to the marginal teeth, are present just inside the anterior end of the lower jaw. The palatal teeth are, typically, adpressed, so much so that some are flattened transversely. The marginal teeth, though not adpressed, are closely spaced. Their bases are overgrown by ridges of bone and the teeth thus fused firmly to the marginal and palatal bones. The teeth are relatively larger and less closely spaced than in *Diplocaulus*.

The lateral line canals are well developed over the face and snout (Fig. 3). The anterior commissure is apparently represented

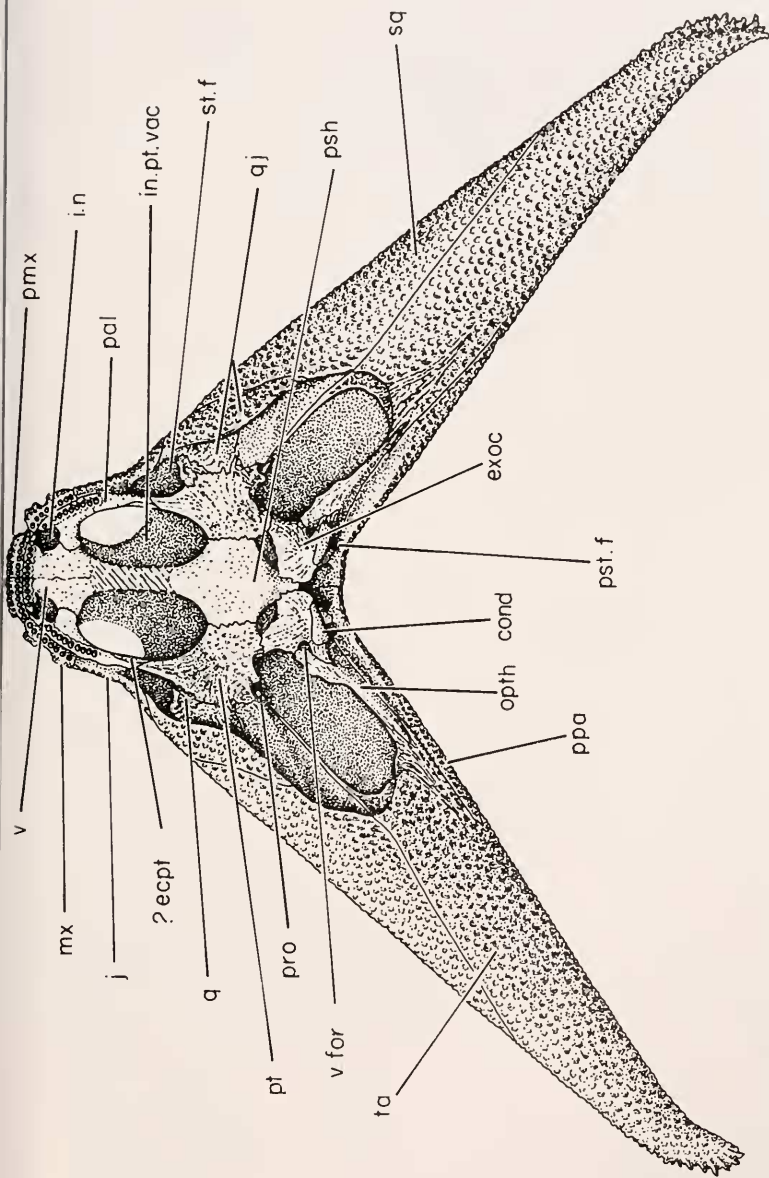


FIG. 2. *Diploceraspis* skull, reconstructed palatal view. Approximate enlargement, x 0.8. Number of teeth shown is incorrect; vomer bears 6 rather than 5, palatine 11 rather than 9. Abbreviations: *cond*, condyle; *expt*, ectopterygoid; *exoc*, exoccipital; *in.n*, internal naris; *in.pt.vac*, interpterygoid vacuity; *oph*, opisthotic; *pal*, palatine; *pro*, prootic; *psh*, parasphenoid; *pst.f*, posttemporal fossa; *pt*, pterygoid; *q*, quadrate; *st.f*, subtemporal fossa; *v*, vomer; *v.for*, vagus foramen; (See caption, Figure 1 for other abbreviations.)

by a deeply sculptured, transverse groove across the anterior surface of the premaxillae. The supraorbital canals, which originate anteromedial to the external nares, pass back and outward to and across the posterior border of the nares. From the nares they continue laterad for a short distance and then curve posteromedially in front and just medial to the orbits. They parallel the medial border of the orbits and terminate near their posterior margin.

The infraorbital canals originate on the maxillae near the narial openings, turn dorsomedial to approach an antorbital commissure with the supraorbital, and curve below the orbits to terminate along the posterolateral face of the jugal. The postfrontal, postorbital, squamosal, and postparietal bear enlarged pits with raised rims which may represent other portions of the lateral line system. On the mandible both oral and mandibular canals are present; the former, rather indistinct, extends along the dentary, parallel and just ventral to the mouth border, and ends near the coronoid process; the mandibular follows the dentary-splenic and dentary-angular sutures to about the midpoint of the mandible, turns ventrad, and disappears.

Skull roof. A complete skull is known from only one specimen, MCZ 3009. In consequence, the description of orbital and preorbital elements is limited to the characteristics of that individual although an incomplete, badly crushed specimen, MCZ 3025, and an eroded, partial skull, CM 8548, check on some of the interpretation (Fig. 1).

In accordance with the unusual form of the skull, the bones of the face are relatively small and somewhat atypic in their relationships. The premaxilla consists of a horizontal, subrectangular plate on the dorsal surface and a short vertical flange that forms the anterior edge of the face, contacts the maxilla below the external naris, and bears seven or eight teeth. The dorsal (horizontal) portion angulates sharply with the anterior part to mark the boundary of the flattened skull roof. In the absence of nasals (see discussion below), the premaxillae contact the prefrontals behind the nares. This relationship is unique among the Keraterpetontidae, but a somewhat similar pattern occurs in *Urocordylus* where the prefrontals extend forward between nares and nasals to contact the premaxillae. Because of the absence of the nasals the premaxillae contact the frontals — a condition approached in *Batrachiderpeton* which has tiny nasals, and duplicated in *Diplocaulus* which also lacks nasals.

Like the premaxilla, the maxilla consists of two sharply angulated elements, a horizontal, subrectangular dorsal plate and a

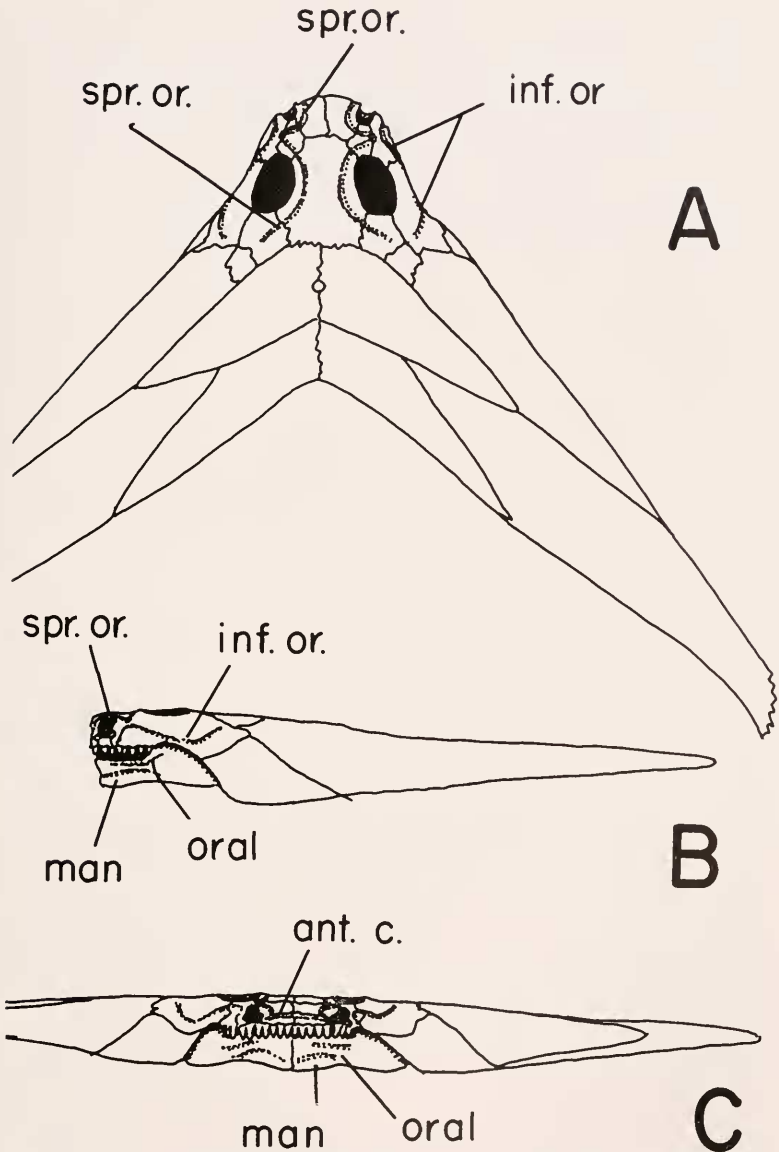


FIG. 3. *Diploceraspis* skull and mandible, reconstructed. A, dorsal; B, lateral; C, frontal view. Approximate enlargement $\times 0.67$. The dotted lines indicate the position of the lateral line canals. Abbreviations: *ant.c.*, anterior commissure; *inf.or.*, infraorbital canal; *man*, mandibular canal; *oral*, oral canal; *spr.or.*, supraorbital canal.

vertical, descending process that bears seven or eight teeth. The horizontal and vertical portions are rather sharply separated by a difference in sculpture and by a deep V-shaped notch that receives the anterior end of the jugal. No suture can be distinguished between the two portions in MCZ 3009, but the possibility remains that the maxilla as described here includes a fused lacrimal bone (see discussion below). The dorsal portion of bone forms the anterolateral border of the orbit and is bounded medially by the prefrontal. The latter relationship occurs also in *Diplocaulus* although in that genus the lacrimal is also present.

The frontals of *Diploceaspis* are fused, at least in the three specimens in which they are known, into a single interorbital plate like those in *Diplocaulus* and *Urocordylus*. I have not been able to detect any trace of midline suture on either dorsal or ventral surface, and the sculpture shows no trace of a dual origin for this element. The anterior contact of premaxillae and frontal was discussed above. As in *Diplocaulus*, the frontal forms most of the medial border of the orbits and separates the pre- and postfrontals, whereas in the other neotrideans these elements contact each other, albeit narrowly, and separate the frontal from the orbits. Watson ascribed this condition in *Diplocaulus* to the dorsomedial shift of the eyes in a very flat skull; presumably the explanation would hold here as well.

A single element lies between the premaxilla, maxilla, and frontal on each side. The immediate question is which of three bones, prefrontal, lacrimal or nasal, is represented here. The bone is vaguely diamond-shaped, forms the posterior border of the external naris, contacts the premaxilla anteromedially and the frontal posteromedially, continues laterad as the anterior border of the orbit, and lies against the maxilla between orbit and naris. It is crossed by a lateral line groove from the maxillary contact, posterior to the corner of the naris, to the frontal suture.

An interpretation of this bone as the nasal seems to me most improbable. In general in the amphibians, the nasals lie side by side along the midline of the snout. The questionable elements in *Diploceaspis* are separated by the premaxillae and frontal. Furthermore, these bones also form the anterior border of the orbits and contact the maxilla — atypic characteristics for the tetrapod nasal. Finally, in other amphibians, the supraorbital lateral line canal passed directly from the premaxilla onto the nasal, but, as indicated, in *Diploceaspis* this canal passes laterad from the premaxilla along the posterior margin of the external naris and continues laterad for a short distance over the maxilla

(or the lacrimal fused to the maxilla) before it turns in and back to cross the bone here described.

The choice then lies between lacrimal, prefrontal or an element formed by fusion of the two. No trace of a suture occurs on either the external or internal surface of the bone; nor does the pattern of surficial pitting show a discontinuity. If this bone was formed by fusion of prefrontal and lacrimal there seems no good reason for the lateral shift of the supraorbital canal to the maxilla. Although the possibility of fusion cannot be totally rejected, it too appears improbable.

The topographic relationships of the bone are such that it might be either the prefrontal which established a maxillary contact with loss of the lacrimal or the lacrimal which has acquired premaxillary and frontal contacts with the loss of the prefrontal. No trace of a groove or tube for the lacrimal duct can be identified, but, since the presence of this structure in other neotrideans has not been confirmed, its absence in *Diploceraspis* may not be significant. The course of the supraorbital lateral line canal is more instructive, however. In other amphibians this canal typically originates on the premaxilla and passes posterolaterad across the nasal. On the nasal it bends sharply laterad, curves across the lacrimal and then swings posteromedial onto the prefrontal and finally onto the frontal. In those forms in which the prefrontal separates nasal and lacrimal, the outward curve may be confined to the prefrontal and the canal lies entirely medial to the lacrimal. In others the canal passes directly from nasal to frontal — here again medial to the lacrimal. In any case the supraorbital lateral line canal crosses or is medial to the lacrimal; it never lies lateral to the lacrimal on the maxilla; but it may be laterad, it may cross, or lie medial of the prefrontal.

As already described, this canal in *Diploceraspis* crosses the posterior end of the naris in front of this questionable bone, curves across the maxilla laterad to it and then turns medial across it just in front of the orbit. If the bone is the lacrimal then the position of the supraorbital canal is unique. If the bone is the prefrontal then the supraorbital canal lies in a normal position. In consequence I interpret this element to be the prefrontal.

Two questions concerning the bones of the snout still remain. Is the nasal fused to the premaxilla (or prefrontal)? Is the lacrimal fused to the maxilla? As to the former question, no trace of a transverse suture or of a change in dermal sculpture appears in the skulls studied. If fusion occurred, it happened early in development, and since the nasals are absent in the similar *Diplocaulus*,

their disappearance here is not unexpected. The problem of lacrimal-maxilla fusion is not so easily settled. Although no complete suture appears, the dorsal portion of the maxilla shows partial separation from the ventral, tooth-bearing part, and bears quite different dermal sculpture. Furthermore, the position of the supraorbital lateral line on this medial portion is very similar to its pattern on the lacrimal in other amphibians. The jugal reaches forward to touch this dorsal element and, indeed, separates it in part from the ventral portion. This element also forms a short part of the anterolateral border of the orbit. If this is the lacrimal, then prefrontal-lacrimal-maxilla-jugal pattern is precisely like that in *Keraterpeton* and quite distinct from that in *Batrachiderpeton* and *Diplocaulus*. In these latter genera, the jugal fails to reach the lacrimal; the lacrimal excludes the prefrontal from the naris and is excluded from the orbit. It differs also from that in *Diceratosaurus*, *Urocordylus*, and *Scincosaurus* but only in that the jugal fails to reach so far anteriorly, a condition probably related to the relative lateroventral position of the orbits in these genera. I conclude from this that the lacrimal is present, is partially fused with the maxilla, and has essentially normal relationships to the other bones of the snout.

The jugal consists of two rather distinct parts, a slender anterior ramus along the lateral border of the orbit and a broader posterior plate. The anterior ramus contacts, as indicated above, the maxilla and the lacrimal and also supports the palatine. The ventral border, forming the upper edge of the mouth is somewhat emarginate (Fig. 4). This anterior extension of the jugal occurs also in *Diplocaulus*, *Keraterpeton*, and, to a lesser extent, in *Batrachiderpeton*. In these forms, however, the maxilla reaches posteriorly for a considerable distance below the anterior ramus, separating it from the mouth. The shape and relationships of the posterior portion are, on the other hand, fairly typical for the neotrideans and differ only because of posterior shift of the postorbital, described in the next paragraph.

The pattern of the postorbital and postfrontal bones is unusual and is duplicated only in *Diplocaulus*. A relatively large pentamerous bone forms the posterior border of the orbit and extends between the medial elements of the skull table, the frontal and parietal, and the anterior lateral element of the cheek, the jugal. A smaller, squarish bone lies posterolaterad to the element just described. This second bone is bounded anterolaterally by the jugal, posterolaterally by the squamosal and posteromedially by the parietal.

The larger, anterior bone shows the essential relationships of the postfrontal in more normal amphibians. Among the other neotrideans the postfrontal-prefrontal contact is typically quite slender, and the two bones in a similar position in *Diplocaulus* are completely separated by the frontal. The lateral contact with the jugal is unusual but is inevitable if the postorbital is lost or "pulled" backward out of the orbit. There is consequently no positive evidence that this bone is the postorbital, and if the smaller element behind it is postorbital (see below), then it must be postfrontal. If the posterior element is the supratemporal, unlikely as that seems, then the identification remains doubtful.

The posterior of these bones in *Diplocaulus* has been termed, variously, squamosal (Case, 1911, p. 86), supratemporal (Williston, 1909), and postorbital (Douthitt, 1917, p. 6; Watson, 1913, p. 960). The topographic relationships of the bone in *Diploceraspis* as well as in *Diplocaulus*, suggest that the latter interpretation is most reasonable. In the typical, "unspecialized," amphibian skull, the supratemporal has broad contacts with parietal, squamosal, and tabular. It also touches the postparietal posteriorly in some and the postfrontal and/or postorbital anteriorly. In no example does the supratemporal contact the jugal. Defined broadly, the supratemporal lies between the squamosal and the parietal and postparietal. The questionable element here does not touch either tabular or postparietal; it does contact the jugal, and, like the postorbital of other amphibians, is bounded laterally by the jugal and squamosal bones and medially by the postfrontal and parietal. The only difference in relationship of this bone from the typical postorbital is the loss of contact with the orbital border. Watson pointed out in 1913 that the postorbital in *Batrachiderpeton* had been carried backward (or the orbit forward) so that the orbital border was much narrowed. In *Urocordylus* the postorbital is also nearly excluded from the orbit and the supratemporal occupies the typical position (Steen, 1938, p. 209). All evidence therefore indicates that this is the postorbital in *Diploceraspis* as well as in *Diplocaulus*.

The remaining elements of the cheek region, the quadratojugal and squamosal, reflect in their size and form the development of "horns." The quadratojugal is roughly trapezoidal, extends along the lateral margin of the skull from the posterior corner of the mouth to a point some distance behind the quadrate, and curves onto ventral and dorsal surfaces of the skull. It joins the jugal anteriorly and anteromedially. A ramus extends medioventrally to contact, in anterior-posterior sequence, the quadrate, pterygoid,

and the ventral ramus of squamosal and to floor the subtemporal fossa (Figs. 2, 4). A large foramen pierces this ramus just laterad of the quadrate. The ventrolateral edge of the quadratojugal forms a continuous line with the squamosal unlike the distinct ventral flange observed in *Diplocaulus*. It also differs from *Diplocaulus* in sharing a pterygoid contact with the squamosal — and thus retains the typical amphibian condition.

The squamosal is a very large triangular bone that forms most of the anterolateral edge of the "horn." The dorsal portion contacts the quadratojugal and postorbital anteriorly, the parietal anteromedially, and the tabular posteromedially. The lateral border curves broadly to the ventral surface and extends some distance posteromedially to contact the tabular again near the midline of the horn, medially to form the lateral border of the otic notch (which is ventral in *Diploceraspis*), and anteromedially to join the quadratojugal (Fig. 2). All of these surfaces are sculptured. In this respect it differs from the *Diplocaulus* squamosal which has much of its ventral surface smooth. It also differs in its relation to the otic notch, for in *Diplocaulus* an anteromedial process of the tabular excludes it from the otic notch. The internal surface of the dorsal plate of the squamosal gives rise to a flange that extends anteroventrally along the internal ramus of the quadratojugal to a broad suture with the pterygoid (Fig. 4). An internal flange extending to the pterygoid occurs also in *Batrachiderpeton* and *Diplocaulus*, and probably, in *Diceratosaurus*. In all, the relationship of the squamosal to the other elements of the skull is normal in spite of the unusual form of the bone. This form results, inevitably, from the forward shift of the quadrate and the development of a "horn" at the dorsal posterolateral corner of the skull.

Of the bones in the temporal series, the inter- and supratemporals and the tabular, only a single element occurs in *Diploceraspis*. This is the principal element of the "horn" and is generally of extremely elongate, trapezoidal form. This bone contacts the squamosal anterolaterally, the parietal anteriorly, and the post-parietal anteromedially. It curves onto the ventral surface both anterolaterally and posteromedially so that the distal end of the bone forms a hollow, flattened cylinder. The characteristic sculpture covers the dorsal and ventral surfaces. This cylinder continues posterolaterally into the recurved tips of the horn. Anterolaterally the ventral plate contacts the ventral plate of the squamosal; it also forms the posterior border of the otic notch, makes

contact with the opisthotic behind the notch and forms an antero-medial juncture with the postparietal.

The bone occupying this position in *Diplocaulus* has been considered by most authorities to be the tabular (Douthitt, 1917, p. 7, and others). Olson (1951, pp. 90-91), however, has argued that it is, rather, the supratemporal. In consequence a brief discussion is necessary here. In the nectridean *Urocordylus*, two temporal elements are present. The anterior of these is a small, slender bone between the squamosal and parietal which makes a short anterior contact with the postorbital and a somewhat wider contact with the posteriad temporal bones. The posterior element forms the posterior corner of the skull table and the medial border of the otic notch, contacts the parietal and postparietal medially, and the squamosal laterally, and, presumably, joins the opisthotic ventrally. These are the typical relations of the supratemporal (anterior element) and tabular (posterior element) in the Amphibia and are so regarded by Steen (1938, p. 207).

Among the other nectrideans, only a single temporal element has been identified, that with the typical relations to squamosal, postparietal, skull table, and opisthotic characteristic of the tabular. The only difference in *Diplocaulus* (and *Diploceraspis*) is the great enlargement of the bone to form the "horn." It is difficult to understand why the supratemporal would assume the position of the tabular and lose its normal relationship to the postorbital, parietal, and squamosal. In consequence, Olson's interpretation is rejected.

Like the squamosal of the cheek region and the tabular of the temporal, the medial bones of the skull roof, the parietal and postparietal, show marked modification in shape and size to form the posteromedial portion of the "horns." They resemble quite closely the homologous elements in *Diplocaulus*. The parietals are narrow, elongate, triangular bones. A moderately large opening appears near the midpoint of the interparietal suture. The flared dorsal end of the epipterygoid is fused to the underside of the parietal (Fig. 4).

The postparietals are, similarly, narrow, elongate triangular bones. They are bordered by the parietals anteriorly and anterolaterally and by the tabular posterolaterally. Each curves a short distance onto the occipital surface and descends to the exoccipital and opisthotic by two short rami separated by a large opening, presumably the posttemporal fossa (see discussion in next section). They also form the dorsal border of the foramen magnum.

Occipital surface. The occipital plate is formed by three elements on either side (Fig. 5). The postparietal bone which covers the dorsal border is described above. The exoccipital bone is relatively large and comprises the condyle, a ventral plate, and two vertical processes, one of which extends directly upward to contact the postparietal and the other of which extends up and out to a rather long juncture with the opisthotic. These two rami are separated by a notch that forms the lower edge of a large oval opening into the skull. The ventral plate is also notched for the inner edge of a foramen immediately in front of the occipital condyle. It contacts the opisthotic again in front of the foramen and continues forward to a junction with the exoccipital ramus of the pterygoid. The length of this suture is somewhat variable from specimen to specimen, but, in all, a rather large ovoid gap is left between pterygoid and parasphenoid contacts. The anteromedial corner of the ventral plate is joined in complex suture with the parasphenoid. Behind this point the margin is free and the two exoccipitals fail to touch along the midline. The base of the occipital condyles lies at the junction of the dorsal rami and the ventral plate. The condylar surfaces are wide, shallow, and fairly flat, rather like 110° segments of a cylinder with its axis nearly perpendicular to the midline. They show very slight transverse curvature and face somewhat mediad so that the head could have been turned only a very short distance sideways.

The inner face of the exoccipital is quite complex. A narrow, horizontal plate forms a shelf along the medial and anteromedial sides of the base of the ascending (postparietal) ramus. The narrow groove between this shelf and the ventral plate is lined with a thin sheet of granulose bone. This sheet may represent the bony cap of the basioccipital cartilage whose presence is suggested by the midline gap between the exoccipitals. If I am correct in this interpretation then the groove and the shelf above represent the basioccipital contact of the exoccipital. Another feature of the inner surface is a strong ridge arising from the opisthotic border just behind the small foramen described above. This extends anteromedially and continues up the anterolateral side of the postparietal ramus. A deep groove lies posterior to the ridge and extends as a fossa into the condylar base. A much shallower groove anterior to the lateral end of the ridge continues laterally into the foramen. The overall shape of the exoccipital and its relationship to the pterygoid, parasphenoid, and postparietal are similar to those of *Diplocaulus* (Douthitt, 1917, p. 12). Although Douthitt did not report an unossified gap between pterygoid and

parasphenoid contacts, it does occur in some *Diplocaulus* specimens. The condyles in *Diplocaulus* curve further ventrally, face more directly posteriad, and are more strongly curved.

The opisthotic is a wedge-shaped bone with a broad medial "head" and a tapering paroccipital process extending laterally. The "head" contacts the exoccipital and extends above that bone on the occipital surface to the postparietal. The dorsal border of the opisthotic is formed by the postparietal, but a slender tongue of the tabular reaches medially from the lateral end of the paroccipital along its dorsal internal border. The "head" of the opisthotic is strongly concave internally and bears a thin, circular sheet of granulose bone. The free, anteroventral border of the opisthotic forms the posterior edge of the otic notch. Although Douthitt reports the exoccipital and opisthotic as fused in *Diplocaulus*, sutures can be distinguished in many specimens of that genus. The character of the opisthotic "head" could not be distinguished in the specimens of *Diplocaulus* available for study, but it appears to bear a rough, "unfinished" inner surface. Like *Diplocaulus* and unlike the other genera (*Urocordylus*, *Scincosaurus*, and *Batrachiderpeton*) in which the character is known, the opisthotic lacks a pterygoid contact.

The openings in the occipital surfaces just described are difficult to interpret. Douthitt (1917, p. 12) described the rather similar occipital structure of *Diplocaulus* and suggested that the small foramina in front of the condyles on the ventral surface served for passage of the vagus but did not offer any interpretation of the larger openings above the condyles. Similar, small precondylar openings occur in *Diceratosaurus*, but none of the available specimens show the occipital area above the condyle. Watson in his description of *Batrachiderpeton* (1913, p. 952) indicated that a foramen above the condyle was the exit of the glossopharyngeal and vagus nerves and that a smaller opening on the ventral surface of the opisthotic just in front of the condyles was the fenestra ovalis. This area has not been described in the other neotrideans.

The upper opening in *Diploceraspis* and *Diplocaulus* is bordered by the postparietal, the paroccipital process of the opisthotic, and the exoccipital. In other amphibians, the rhachitomes for example, this is the position of the posttemporal fenestra. I see no reason to consider it otherwise in *Diploceraspis*. Since Watson did not discuss the relation of the upper opening to the bony elements of the occiput in *Batrachiderpeton*, no conclusion can be offered here on that genus. The foramen for the vagus (and associated nerves)

in the amphibians pierces the occipital surface obliquely above the condyle, and is directed posterolaterally rather than directly to the rear. It opens along the suture between the opisthotic and exoccipital somewhat posterior to the fenestra ovalis. If one rotates the ventrolateral portions of this typical occiput under and forward with a corresponding rotation of the otic notch and the quadrate, the opisthotic forms the ventral edge of the occiput, lateral to the condyles, and the ventrolateral portion of exoccipital-opisthotic contact would come to lie on the ventral (palatal) surface of the skull. The otic notch would then be in front of the opisthotic rather than below and outside it, and the fenestra ovalis and vagus foramen would open ventrolaterally rather than posterolaterally. This is precisely the condition in *Diploceaspis* and *Diplocaulus*. Douthitt's conclusion that the ventral precondylar foramen of *Diplocaulus* was the vagus nerve opening is thus substantiated by the morphology of the *Diploceaspis* occiput.

Palate — Basicranium. The palate of *Diploceaspis* (Figs. 2, 4, 5) shows many of the features typical of other specialized amphibians with flattened skulls (Watson, 1951, pp. 46-49) — reduction of the basioccipital and basisphenoid, development of large interpterygoid vacuities, a corresponding reduction of the palatal ramus of the pterygoid, shift of the quadrate anteriorly of the occipital condyles, development and lengthening of a parasphenoid-pterygoid suture, and the appearance of pterygoid-exoccipital and parasphenoid-exoccipital contacts. In these characteristics *Diploceaspis* parallels *Diplocaulus* and departs from the pattern of the less modified neotridians. On the other hand, they are anticipated in some genera, for example *Diceratosaurus*, so that they represent a logical continuation of a trend.

The vomers, separated by an indistinct midline suture, form the medioanterior portion of the palatal complex. Each bone is roughly quadrangular, lying against the premaxilla anteriorly, forming the medial border of the internal naris, contacting the palatine laterally, forming the anteromedial border of the interpterygoid vacuity, and joining the parasphenoid posteriorly. Each vomer bears a row of six teeth along its anterior border. These lie in line with and continue the arc of the palatine teeth.

The palatine is a delicate triradiate bone. Its anterolateral border is braced against the maxilla, and it extends a narrow tooth-bearing process forward along the latter bone almost excluding it from the border of the internal naris. A rather broader but short process extends medially behind the internal naris to make a loose contact with the vomer. The base of this process bears an internal

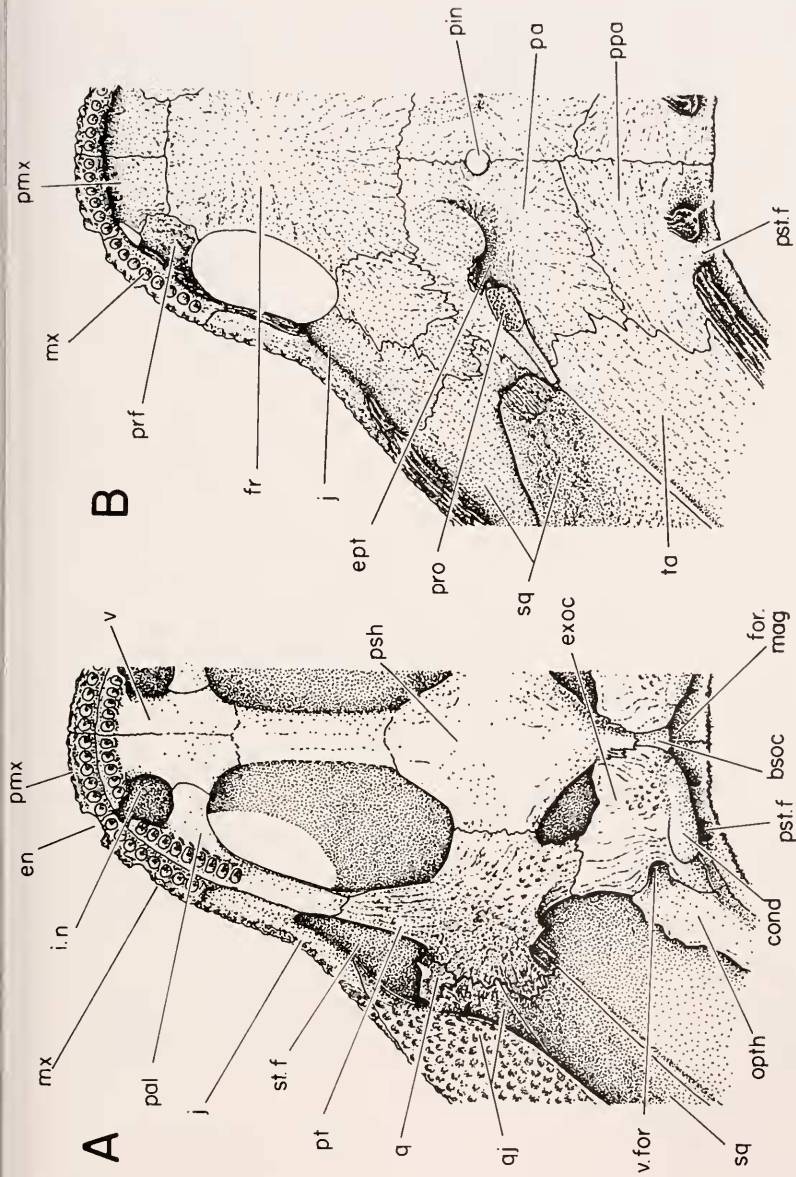


FIG. 4. *Diploceraspis* skull, reconstructed palatal details. Approximate enlargement x 1.5. A, Palatal elements in place. B, Palatal elements removed to show undersurface of skull roof. Abbreviations: *bsoc*, basioccipital; *ept*, epipterygoid; *for.mag*, foramen magnum. For other abbreviations see captions, Figures 1 and 2. Number of teeth shown incorrectly: vomer bears 6 rather than 5; palatine 11 rather than 9.

facet that braces the bone dorsally against the prefrontal. The third process extends posteriorly to contact the pterygoid — this portion is also braced dorsally by an extensive suture with the jugal. The eleven or twelve teeth lie in an arcuate row just inside the maxillary contact. The vomerine and pterygoid rami form the anterior and anterolateral borders of the interpterygoid vacuity; the pterygoid ramus also forms a short segment of the border of the subtemporal fossa.

The ectopterygoids have not been definitely identified but may be represented by a short, tiny splinter of bone at the palatine-ptyerygoid suture.

The pterygoid is a moderately large bone vaguely quadriradiate in ventral aspect. The palatine ramus is a narrow tongue of bone joined in a complex, jagged suture with the palatine. The short, wide, lateral ramus contacts the quadrate, quadratojugal, and squamosal successively in a continuous, jagged suture. The posterior ramus forms a contact with the exoccipital, and the medial ramus with the parasphenoid. The internal, dorsal, surface of the pterygoid bears a ridge-like ascending process that extends from the posteromedial corner of the palatine ramus to the posterolateral corner of the lateral ramus. This process abuts anteromedially against the epipterygoid (see below) in a complex suture and continues posterolaterad in contact with the prootic (and possibly the parietal as well) to or near the squamosal-tabular end of that element. The posteromedial face of this ridge is deeply concave — a concavity which is accentuated by a parallel ridge which lies just mediad of the base of the ascending process. The ridge is also modified by a deep notch just behind the epipterygoid contact. The ventral, external, surface of the pterygoid is marked by a short flange projecting posteriad between the lateral and exoccipital rami into the otic notch. This flange is variously developed in *Diploceraspis*, extends as a continuation of the lower surface of the lateral ramus and roofs a shallow groove that runs anterolaterad along the posterior border of the exoccipital ramus. The exoccipital contact is fairly short and is probably separated in all *Diploceraspis* from the pterygoid-parasphenoid and the exoccipital-parasphenoid contacts by a moderately large vacuity. It differs significantly from the pterygoid of *Diplocaulus* only in the presence of a quadratojugal contact.

The parasphenoid comprises a posterior, moderately thick, diamond-shaped plate, which contacts the pterygoids and exoccipitals on either side and forms the posteromedial borders of the interpterygoid vacuities, and a narrow, thin, anterior ramus,

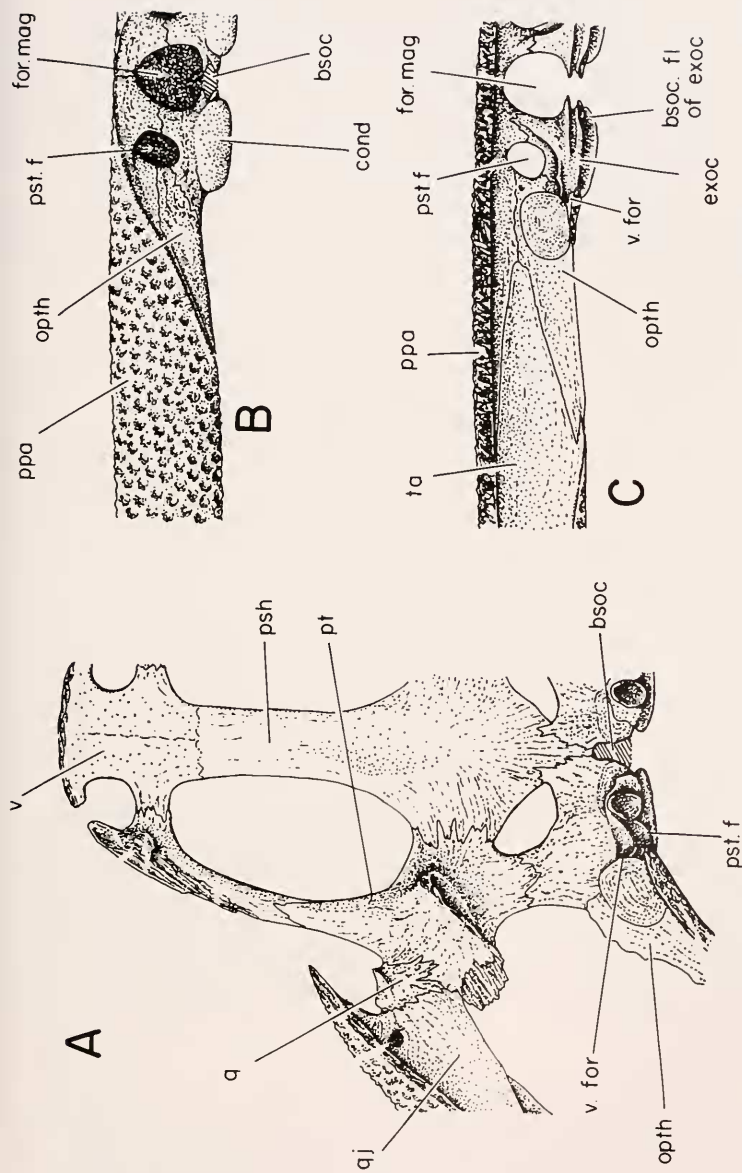


FIG. 5. *Diploceraspis* skull, reconstructed palatal and occipital details. Approximate enlargement, x 1.5. *A*, Dorsal (internal) view of palatal elements. *B*, Posterior view of occiput. *C*, Anterior (internal) view of occiput. Abbreviation: *bsoc. fl. of exoc*, basioccipital flange of exoccipital. For other abbreviations see captions, Figures 1, 2, and 4.

which extends forward between the vacuities to the vomers. The posterior tip of parasphenoid extends a short distance backwards between the exoccipitals and may represent an ossified portion of the basisphenoid.

The quadrate is a small element, lying entirely on the ventral surface, and is triangular shaped, with apex posteriad, in ventral aspect. The medial leg of the triangle forms a complex suture with the pterygoid, the lateral leg with the quadratojugal. The base of the triangle forms a trochlear condyle facing anteroventrad. The inner (dorsal) surface is likewise triangular but it extends posteriad as a thin sheet of bone over the quadratojugal and pterygoid to approach the squamosal.

The epipterygoid is apparently represented by a short process that extends from the ascending process of the pterygoid to the parietal, and then spreads as a horizontal sheet anterolaterad over the inner surface of the latter bone. Since in all specimens, some seven or eight partial skulls, this sheet is fused to the parietal, some question of identity remains, and it may be interpreted as a descending process of the parietal. In all specimens, however, the anterolateral borders of the sheet form a sharp margin and define a layer of bone distinct from the parietal. Moreover, the position of this element is lateral to the ascending ramus of the pterygoid, and the vertical process extends a considerable distance down along the lateral side of this pterygoid ramus — the proper position for the epipterygoid. Posteromedially it touches the small element here interpreted as an ossified portion of the prootic as does the epipterygoid in other, more "normal" amphibians. Between the prootic and epipterygoid is a distinct notch, presumably for the passage of branches of the trigeminal. In summary, this bone possesses the proper topographic relationships for the epipterygoid and varies from that bone in other amphibians only in its extensive dorsal fusion with the parietal. In the very flat shallow skull of *Diploceraspis* some bracing of palate against skull roof would seem essential, and the modification of epipterygoid for this function seems reasonable. Douthitt (1917, pp. 11-12) found a similar element in *Diplocaulus*.

FIG. 6. Variation in *Diploceraspis* skulls. All enlarged, x 0.7. *A*, MCZ 3010, dorsal view; left horn, left postparietal, right horn including exoccipital, pterygoid, and quadrate. *B*, CM 8544, *Diploceraspis conemaughensis*, ventral view; left horn including portions of exoccipital and pterygoid. *C*, CM 8548, ventral view; left horn and portion of face, details poorly preserved. *D*, MCZ 3013, dorsal view; left horn including pterygoid. *E*, MCZ 3032, probably

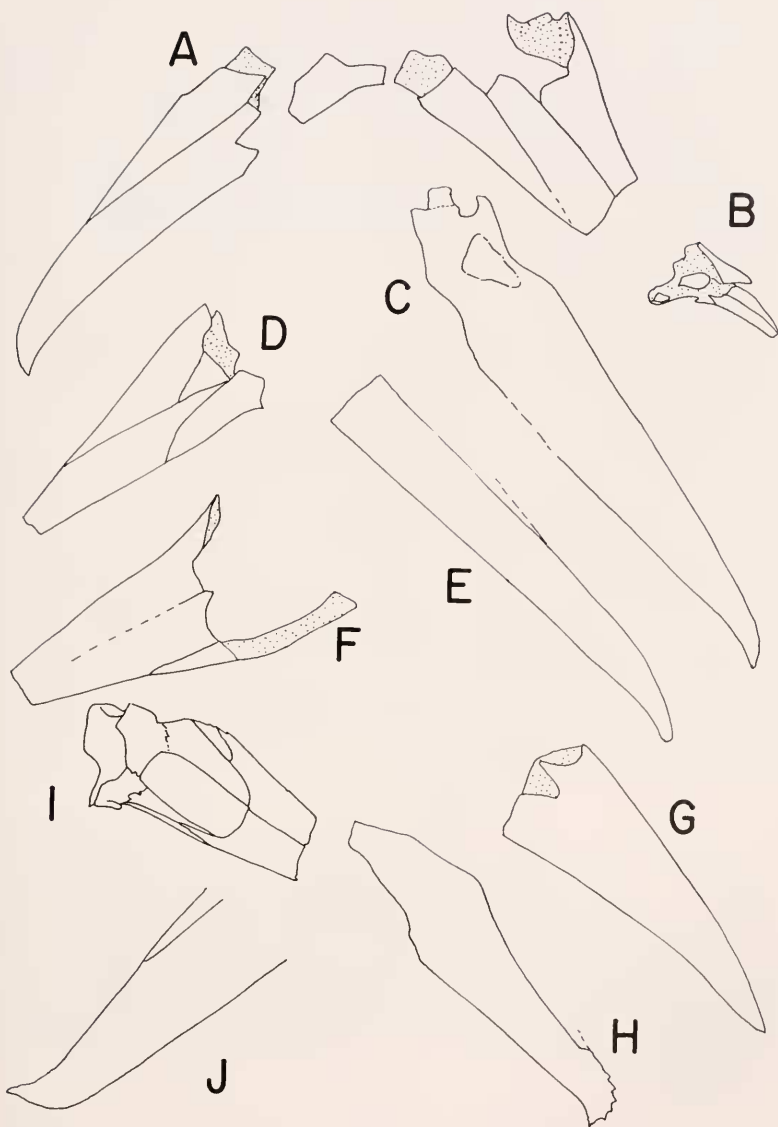


FIGURE 6

ventral view of the left tabular. *F*, MCZ 3026, ventral view; right horn. *G*, MCZ 3017a, dorsal view; right horn. *H*, MCZ 3017b, dorsal view; right tabular and portion of squamosal. *I*, MCZ 3019, ventral view; left horn including exoccipital, partial pterygoid, epipterygoid, and prootic. *J*, MCZ 3009, dorsal view; tip of left horn of complete skull.

On one side of specimen MCZ 3009 and in the partial skull, MCZ 3019, a small spoon-shaped bone lies against the inner surface of the parietal, posteromedial to the ascending ramus of the pterygoid (Fig. 4). The "bowl" of the "spoon" is covered by a thin sheet of granulose bone similar to that on opisthotic and occipital described above and faces posteroventrad. The anterior tip of the "bowl" touches the epipterygoid; the anteroventral edge of the "bowl" and of the "handle" articulate with a facet on the ascending process of the pterygoid; the posterodorsal edge of the bone fits in a facet on the under surface of the parietal; and the "handle" of the "spoon" extends out and back to approach, if not actually touch, the squamosal and tabular. If the element, here interpreted as the epipterygoid, is correctly identified, then the bone just described must be an ossification in the chondrocranium — certainly it has the expected relationships for the prootic. The only alternative interpretation is that of epipterygoid, and its position, posteromedial to the pterygoid, does not support this hypothesis. The apparent absence of this element in most *Diplocaeraspis* skulls may be due to accidents of preservation and preparation as well as variation in ossification from individual to individual. In most *Diplocaeraspis* specimens the otic notch and interior of the skull were filled with fish scales and fragments of bone. Since the prootic element is rather delicate, loosely attached, and of the same size as the fragments in this bone "hash," it could be easily removed inadvertently during preparation — I know this to be true of one specimen.

MANDIBLE

The general modification of skull form in *Diplocaeraspis* conditioned the shape and character of the mandible. Although no intact mandible has yet been recovered, a number of fragmentary specimens (MCZ 3011, MCZ 3014, MCZ 3006, MCZ 3004 and MCZ 3031) provide adequate information for a reconstruction (Fig. 7). The mandibular arch is short and broad, like that of *Diplocaulus*, but the posterior "legs" of the arch are subparallel rather than divergent. It bears a short tooth row, typically 12 teeth on either side. Three or four coronoid teeth are also present. The jaw is relatively deep and bears a relatively high coronoid process. The retroarticular process is also well developed. It lies in line with the ventral edge of the jaw and the circular facet for muscle insertion faces ventrolaterad. In these three features the *Diplocaeraspis* departs markedly from the pattern of *Diplocaulus*.

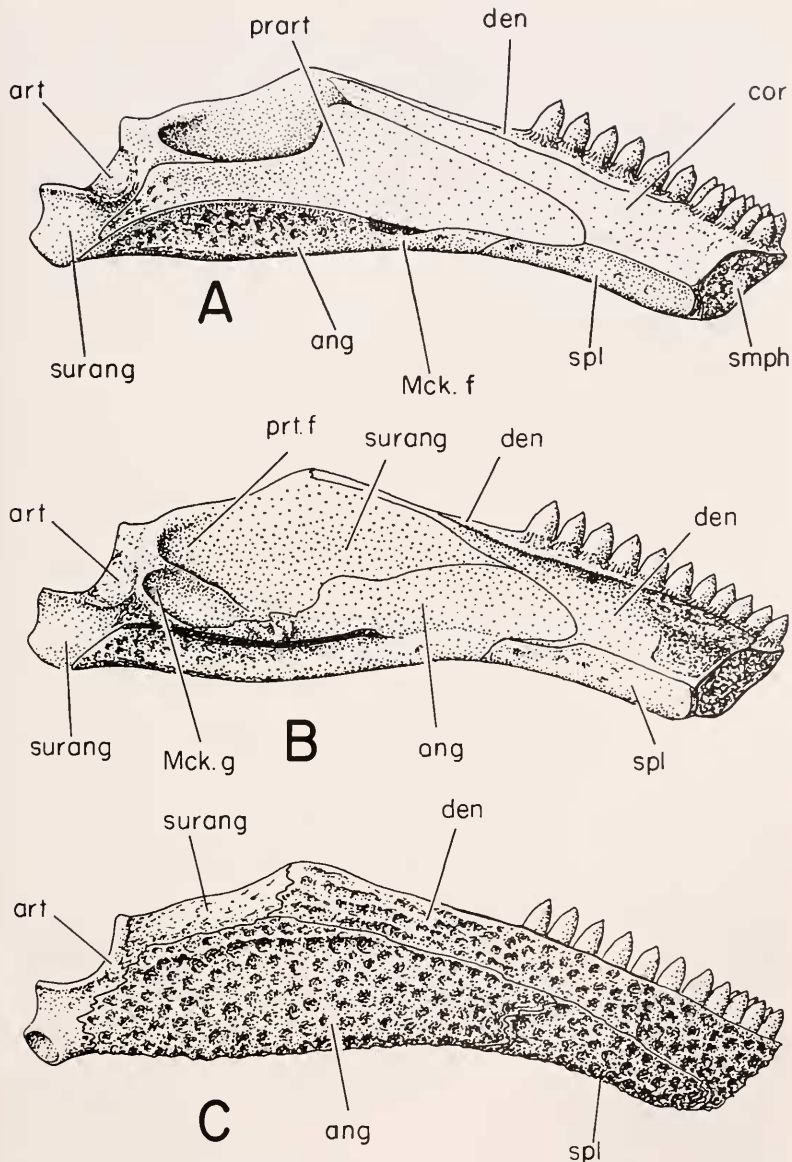


FIG. 7. *Diploceraspis*, reconstructed mandible. Approximate enlargement $\times 2.3$. *A*, Medial view, all elements in place. *B*, Medial view, inner elements removed. *C*, Lateral view. Abbreviations: *ang*, angular; *art*, articular; *cor*, coronoid; *den*, dentary; *Mck. f*, Meckelian fenestra; *Mck. g*, Meckelian groove; *prart*, prearticular; *prt. f*, prearticular fossa; *smph*, symphysis; *spl*, splenial; *surang*, surangular.

The prearticular fossa is relatively short but otherwise normal. Some specimens show a distinct bony node at the bottom of the fossa, presumably a muscle attachment. The articular fossa is double faceted to receive the trochlear condyle of the quadrate and is very low on the jaw — so low that it is below the level of the tooth row as well as the coronoid process. The lateral facet faces posterodorsally, the medial posteromedially. The articulation, therefore, differs radically from that of *Diplocaulus* which faces posteromedially. The inner surface of the jaw is pierced near its ventral margin by a large Meckelian foramen, between the angular and prearticular. I have been unable to distinguish an anterior Meckelian foramen. The inner surface of the surangular bears a deep groove for the Meckelian cartilage. This apparently continued forward, sheathed laterally and ventrally by the angular and medially by the prearticular, to end in a sheet of granulose bone near the anterior end of the dentary. The symphysis is broad but not tightly sutured, for all the jaws observed have separated at this point. The external surface of the mandible is finely pitted; the lateral line canals are described in the preceding section (p. 50).

The articular is presumably represented by the articular fossa, but no suture separates it from the surangular. The latter bone has a very small lateral exposure, forming the dorsal border of the jaw behind the coronoid process and the retroarticular process, but it spreads broadly over the inner surface of the angular, inside the prearticular fossa. Douthitt (1917, p. 15) did not distinguish the surangular from articular in *Diplocaulus*; if most of what he called articular is surangular then the general relationship is the same even though the surangular has a much more extensive lateral exposure.

The *Diploceaspis* angular, conversely, has a broad lateral exposure and a relatively narrow medial one — much narrower than that of *Diplocaulus*. The *Diploceaspis* jaw also differs from that of *Diplocaulus* in the presence of one instead of two splenial elements. The splenial extends halfway up the outer surface of the jaw but has only a very narrow flange exposed on the inner surface. This reverses the condition observed in *Diplocaulus*. In *Diplocaulus* the splenial enters into the symphysis, but it fails to do so in *Diploceaspis*.

The dentary is relatively long, reaching back to the summit of the coronoid process, but is quite shallow. The coronoid consists of a long, narrow posterior arm extending anteriorly along the inner margin of the dentary from the coronoid process, and of a broad

sheet of bone over the inner surface of the jaw below the tooth row. The prearticular, similarly, comprises a slender posterior ramus that reaches back between the surangular and angular to the base of the retroarticular process and a deeper anterior portion that covers the inner face of the jaw in front of the prearticular fossa and below the coronoid process. Comparison with *Diplocaulus* is difficult because the coronoid has not been distinguished in that genus. Douthitt suggested, however, that the coronoid was represented by a narrow splint of bone paralleling the inner border of the tooth row. If he is correct, *Diplocaulus* differs in this respect from *Diploceraspis*, which has a large coronoid spread broadly over the anteromedial surface of the jaw.

AXIAL SKELETON

As indicated by Romer (1952, p. 71), *Diploceraspis* vertebrae are characterized by strong sculpture along the crest of the neural spine and by a pattern of fine, vermiculate lines on the centra (Fig. 9). They agree with *Diplocaulus* in the latter characteristic but differ in the former, for the spine in *Diplocaulus* bears a distinctive pit on an otherwise unornamented crest.² The sculpture is somewhat like that of *Diceratosaurus*, but unlike the latter genus the dorsal ends of the spine are not strongly expanded, and the sculpture consists of elongate pits and anastomosing ridges rather than circular pits. The vertebrae are of lepospondylous type consisting of a coossified centrum and neural arch. The centra are amphicoelous — the cross-section is shaped like an hourglass. Since no articulated skeletons are known, the number of vertebrae is indeterminate.

The anterior, "atlas," vertebra (Fig. 8A) bears a pair of nearly flat glenoid cavities to receive the occipital condyles. A short spine juts forward between these glenoid facets. The neural arch extends well anteriorly above facets and spine to cover the top and sides of the neural canal where it passes into the foramen magnum. No transverse processes are present; presumably no ribs were borne. The ventral surface of the centrum bears an indistinct median keel anteriorly that terminates in the interglenoid spine. The neural spine extends posteriorly, above the postzygapophyses, to fit into a zygantrum on the succeeding, "axis," vertebra. Accessory apophyses above the postzygapophyses also extend posteriorly to embrace the sides of the neural arch of the "axis." The neural

²A few *Diplocaulus* arches show a fine sculpture not very different from that of some *Diploceraspis*.

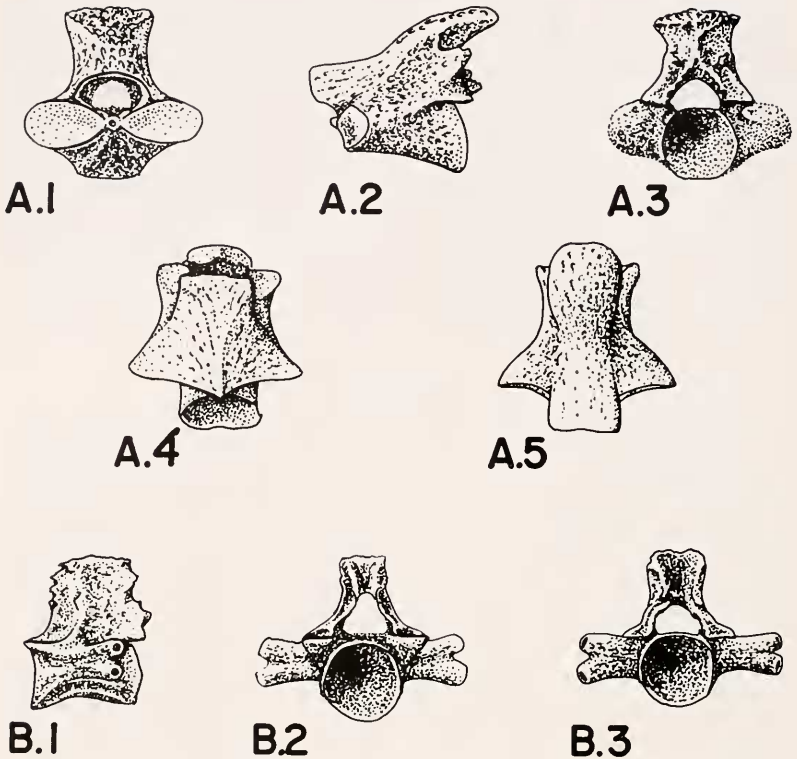


FIG. 8. *Diploceraspis*, "atlas" and "axis" vertebrae. Approximate enlargement, $\times 2.3$. A, "Atlas." A.1, Anterior view; A.2, lateral view, anterior to left; A.3, posterior view; A.4, ventral view, anterior up; A.5, dorsal view, anterior up; B, "Axis." B.1, Lateral view, anterior to left; B.2, anterior view; B.3, posterior view.

spine is far more strongly developed than in *Diplocaulus* and the zygapophyses face ventrally rather than posteroventrally. Otherwise, the "atlas" agrees with that of *Diplocaulus*; it has not been described in the other neotrideans.

The "axis" (Fig. 8B) is distinguished from the remaining vertebrae by the presence of an anterior zygantrum (for the zygosphene of atlas) in the place of a zygosphene. This centrum is also relatively short (its length is only about $2/3$ the height of the vertebra) as compared with the thoracic vertebrae (which are longer than high). The transverse processes extend posterolaterally to

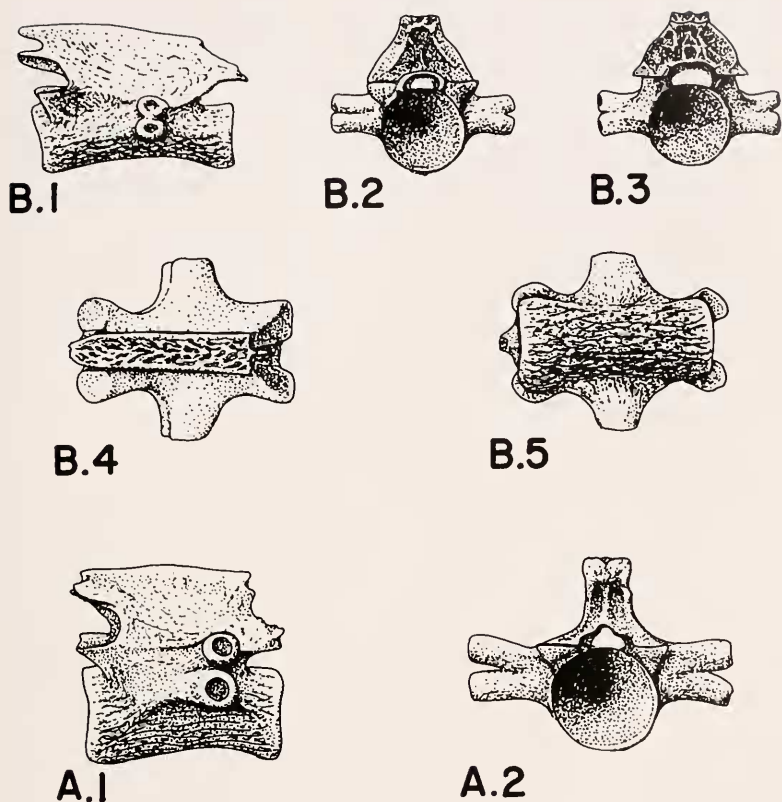


FIG. 9. *Diploceraspis*, "trunk" vertebrae. Approximate enlargement, x 2.3. A, Anterior "trunk" vertebra. *A.1*, Lateral view, anterior to left; *A.2*, anterior view. B, Posterior "trunk" vertebra. *B.1*, Lateral view, anterior to left; *B.2*, anterior view; *B.3*, posterior view; *B.4*, dorsal view, anterior to left; *B.5*, ventral view, anterior to left.

separate, near their distal ends, into distinct dia- and parapophyses. As in *Diplocaulus*, these processes are both borne on the centrum, and the articular facets lie one above the other.

The thoracic vertebrae vary considerably in character, probably as a consequence of individual as well as regional differences (Fig. 11). The anterior thoracics, on analogy with *Diplocaulus*, should be relatively short and high. Figure 9A shows a vertebra of this type; Figure 9B is of a longer, lower vertebra that is, presumably, a posterior thoracic. All the anterior thoracic vertebrae and the

majority of the posterior bear both dia- and parapophyses; a few, perhaps 10 per cent, of the latter have a single transverse process on either side. The diapophysis and parapophysis typically coalesce at their bases; in some they separate only near their distal ends; in others they are distinct to the point of basal coalescence. The articular ends of these processes are typically round or slightly flattened. Each one has a central canal that opens terminally in the center of the articular facet. As in the "axis," the articular facets lie one above the other. The basal portion of the diapophysis lies at the upper border of the centrum and is connected by ridges to the zygapophyses. The basal portion of the parapophysis lies near or slightly above the middle of the centrum and extends in low ridges, a long anterior and a short posterior, along the sides of the centrum.

The articular surfaces of the zygapophyses are horizontal or nearly so. They are complemented by complex articulations between the neural arches and spines. The anterior tip of the neural spine forms a zygosphene that fits onto the posterior end of the neural spine of the preceding vertebra. The ventral surfaces of the zygosphene, directed laterally as well as ventrally, extend posteroventrad to the posterior end of the prezygapophyses. These surfaces are embraced by zygantra extending the sides of the neural arch of the preceding vertebra. The posterior end of arch and spine, of course, bears complementary hollows and projections. As a consequence of the horizontal position of the zygapophyses and the presence of accessory articulations on the neural arch and spine, vertical bending of the backbone must have been very limited. The articulations above the zygapophyses on the neural arch also must have had limited lateral bending — but to a much lesser extent. The medial edges of the prezygapophyses are connected by a sheet of bone that roofs the anterior end of the neural canal. This "roof" fits into a recess between the post-zygapophyses of the preceding vertebra and provides a continuous dorsal shield over the spinal cord. No such structure is observed in *Diplocaulus*.

In *Diplocaulus*, the seventeenth (Case, 1911, p. 88) or eighteenth (Douthitt, 1917, p. 18) vertebra has an unusual form. The neural arch and centrum have the typical elongate character of the immediately preceding thoracics, but the neural spine is relatively low. The centrum, like that of the three or four preceding vertebrae, bears a strong, undivided transverse process with a single broad articular facet. The posterior ventral surface of the centrum, however, bears a pair of heavy spines. These are directed strongly

posteriad to extend behind the end of the centrum, and, in some if not all individuals, join ventrally to form a distinct haemal arch. The posterior tip of the arch fits against or into the end of the haemal arch of the succeeding vertebra. Both Case and Douthitt interpret this to be the sacral vertebra.

Romer (1952, p. 71) described a somewhat similar *Diploceraspis* vertebra with the two posteroventral spines although these did not join to form an arch (CM 8555). Another vertebra (MCZ 3006) of this type appears in the new collection. At least five other vertebrae (MCZ 3021) of otherwise similar character show fusion of these spines (Fig. 10A) to form a strong haemal arch projecting posteriad as in *Diplocaulus*. Romer interpreted this vertebra as the anterior caudal — in the absence of an articulated skeleton neither alternative can be rejected.

A few *Diploceraspis* caudal vertebrae bear short transverse processes or articular facets for caudal ribs (Fig. 10B). Two specimens, one large, the other very small, have short, distinct, undivided transverse processes, and relatively high neural arches and deep haemal arches. These arches are unusually robust and are somewhat swollen laterally. The haemal spines bear deep anterior recesses. The presence of rib articulations suggest that these represent anterior caudal vertebrae. The recess in the haemal spine appears of proper size to receive the posteriorly directed spine of the "sacral" vertebra. The first caudal vertebra of *Diplocaulus*, as described by Case, also has expanded arches and is the last to bear a transverse process. In consequence, I interpret these atypical vertebrae to be the anterior ones of the caudal series.

The remaining caudal vertebrae show great variation (Fig. 10C) — presumably, primarily regional differentiation. Relatively large, flat vertebrae with large neural and haemal arches probably represent anterior caudals because of their similarity to the anterior caudals of *Diplocaulus*. Occurrence of two specimens with indistinct rib facets suggests that the second caudal may also have borne a short rib. The zygantrum and zygosphene are weakly developed, and the zygapophyses relatively small. In some at least the tips of the haemal arches may have been in contact. In several, the sides of the arches bear shallow, vertical grooves. The posterior caudals are long and slender. Both arches and spines are low, and the vertebrae are nearly quadrangular in cross-section. The zygapophyses are very weak or undeveloped. No specimens with unroofed neural and haemal canals have been recognized, but otherwise they resemble the caudal vertebrae of *Diplocaulus*.

Only a few ribs are known in association with *Diploceraspis* material. These are, of course, double-headed, one head above the other, and fairly straight. In the absence of articulated specimens, an estimate of their length relative to body size is impossible

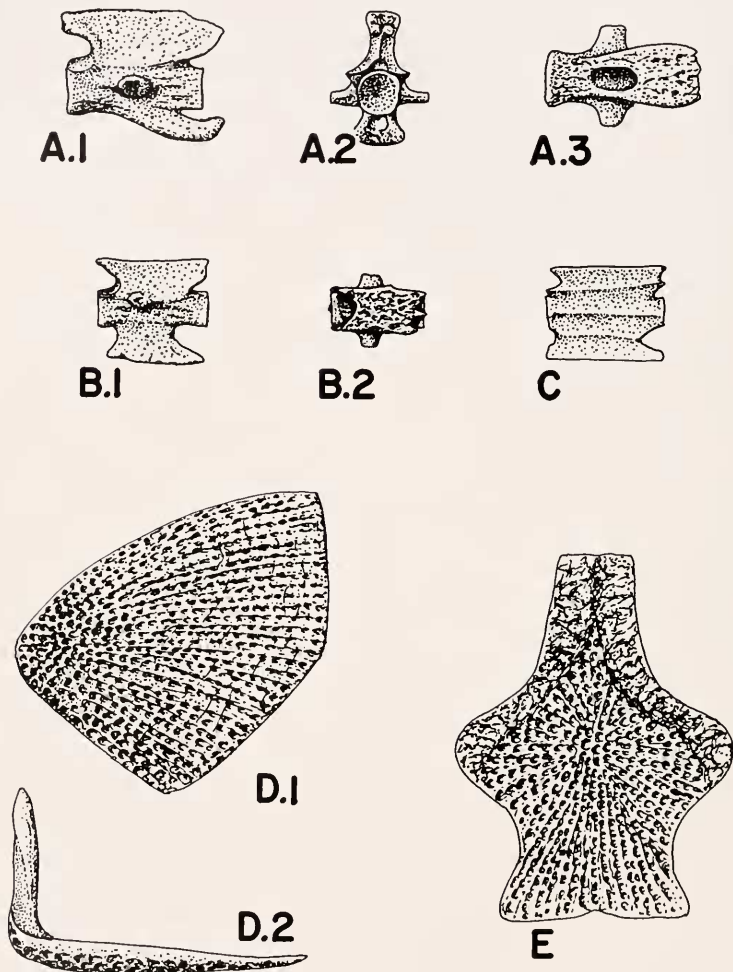


FIG. 10. *Diploceraspis*, caudal vertebrae and pectoral girdle. Approximate enlargement, x 23. *A*, First caudal. *A.1*, Lateral view, anterior to left; *A.2*, anterior view; *A.3*, ventral view, anterior to left. *B*, Anterior caudal. *B.1*, Lateral view, anterior to left; *B.2*, ventral view, anterior to right. *C*, Posterior caudal, lateral view, anterior to right. *D*, Right clavicle. *D.1*, Ventral view, anterior up; *D.2*, anterior view. *E*, Interclavicle, ventral view.

though one must expect that, like those of *Diplocaulus*, they were long.

I have already described the remarkable similarities in the axial skeleton of *Diploceraspis* and *Diplocaulus*. In the presence of both dia- and parapophyses and in the sculpture of the centra, they stand distinct from the other neotrideans. Unfortunately, the vertebrae of *Batrachiderpeton* are unknown. The vertebrae of *Urocordylus*, *Scincosaurus*, *Keraterpeton* and *Diceratosaurus* all possess accessory articulations above and/or below the zygopophyses, but these differ in detail from those of *Diploceraspis*. In all, the ribs are either single-headed or, if double-headed, the capitulum articulates with a facet on the centrum rather than on a long parapophysis. In none do the centra show the complex sculpture of fine lines and pits. A single, suggestive exception occurs in two *Diceratosaurus* vertebrae associated with MCZ 2331. One of these, seemingly an "atlas," shows traces of vermiculate sculpture on the centrum, widespread glenoid cavities, an anteriad extension of the neural arch and a posterior zygosphene. The neural spine is vertical rather than sloping strongly to the rear as

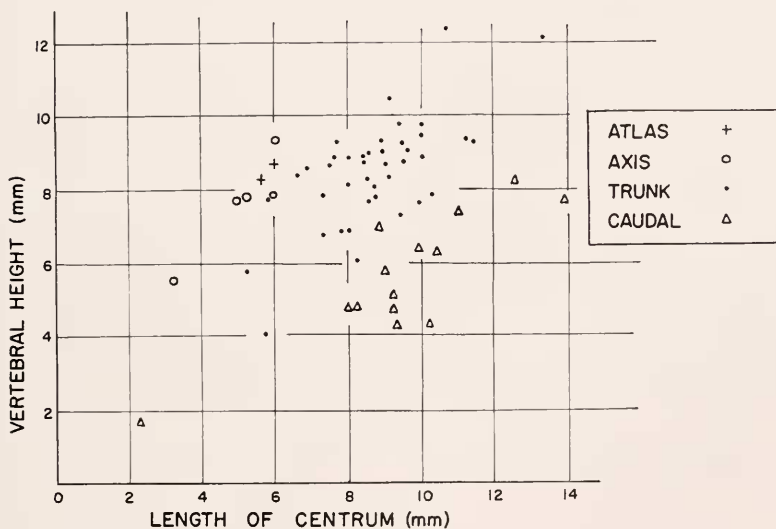


FIG. 11. *Diploceraspis* vertebrae, scatter diagram of length versus height. Length was measured along midline of ventral surface of centrum. Height was measured from the ventral edge of the posterior end of the centrum to the highest point of the neural spine.

in *Diploceraspis*. The second, an "axis," has both posterior and anterior zyganchra and a strong, apparently double transverse process. The centrum, unfortunately, is not exposed.

APPENDICULAR SKELETON

Only two appendicular elements, clavicle and interclavicle, can be assigned with certainty to *Diploceraspis* (Fig. 10D, E). Other recognizable bones from the pectoral and pelvic girdles and limbs are rare in the present collection, and none of the better preserved ones belong to *Diploceraspis*. From analogy with *Diplocaulus* one would expect the limbs to be small, weak, and poorly ossified. The absence of identifiable remains provides support — if only by negative evidence — for this presumption.

The clavicle, described by Romer (1952, p. 70), is of typical neotridian form. The ventral plate is triangular to subrectangular in shape and is finely sculptured on its external (ventral) surface. The sculpture consists of medium to large circular or elongated pits on the lateral corner and smaller pits arranged in rows radiating from the lateral corner toward the midline. Individual variation in sculpture pattern is rather large. The ascending process is a slender rod extending directly upward from the lateral angle of the triangle. The sides of the process are striated vertically.

The interclavicle is roughly pentamerous. A fairly slender process extends anteriorly above the anteromedial edges of the clavicles. This process expands behind the posteromedial edges of the clavicles to form short, broad, lateral processes. Posteriorly to these processes the interclavicle is constricted and extends some distance posteriorly. The sides of this portion are straight and parallel in some specimens; in others, the posterolateral corners flare laterally. The posterior border is straight. The central and posterior portions of the ventral surface are covered by fine pits, circular anteromedially, radially elongate toward the edges of the bone. The anterior margins and anterior process are striated ventrally to receive the dorsal surface of the clavicles. The shape resembles that of *Diplocaulus*.

GROWTH AND DEVELOPMENT

Although available specimens show a wide range of size, their fragmentary character makes precise comparison of growth changes impossible. The small *Diploceraspis conemaughensis* specimen, CM 8544, has well developed horns, apparently much larger than those of *Diplocaulus* in the same size range. This

precocious development is reflected in Figure 14 as shown in tabular length; the large *D. burkei*, MCZ 3009, has relatively longer horns than a *Diplocaulus* twice its size, and the tabulars of MCZ 3009 are twice as long as those of *Diplocaulus* of the same size. In both *Diplocaulus* and *Diploceraspis*, growth rates at the posterolateral corners of the skull were far greater than the "normal" nectrideans and accelerated late in development. *Diploceraspis*, however, shows a markedly different growth rate than *Diplocaulus* in spite of the overall similarity; the allometry of horn on skull size is distinct in the two genera.

The direction of horn growth shows a similar difference. The angulation of the horns decreases in *Diploceraspis* with growth, shows negative allometry, and demonstrates acceleration of posteriad growth relative to laterad in late stages. *Diplocaulus* skulls, however, show positive allometry with acceleration of laterad growth in late stages.

COMPARATIVE DISCUSSION AND SUMMARY

Table 3 summarizes the morphology of *Diploceraspis* as well as comparative features of other nectrideans. *Diploceraspis* and *Diplocaulus* are close in general form and many details but differ in other details, particularly in the topography and proportions of the "face-snout" region and in the character of jaws and tooth row. The keraterpetontids show unity in skull topography and proportions with the exception of characteristics related to flattening of the skull and enlargement of the horns. *Urocordylus* differs importantly in skull characteristics. Comparison of early growth stages indicates that the divergence is related to developmental rates since an immature *Urocordylus* differs very little in skull form from an immature keraterpetontid.

FUNCTION AND ADAPTATION

GENERAL

As already indicated (p. 60), flattening of skull and body and accompanying skeletal modifications are common trends in amphibian evolution. Watson (1951, pp. 53-78) has analyzed the functional significance of these modifications, and presumably his interpretations hold in large part for *Diploceraspis* and *Diplocaulus*. These two nectrideans, however, differ from the others in the presence of horns, in the extreme anteriopad shift of the jaw articulation, and in ventral rotation of the occipital surface.

TABLE 3
COMPARATIVE MORPHOLOGY OF KERATERPETONTIDS

CHARACTER	DIPLOCLERASPIS	DIPLOCAULUS	DICERATOSAURUS	KERATERPETON	BATRACHIDERPETON	URCORDYLUS	SCINCOSAURUS
Skull form	flattened, cornuate	flattened, cornuate	slightly flattened, short horns	slightly flattened	slightly flattened, short horns	deep, no horns	slightly flattened, no horns(?)
Snout/Skull proportions	short	short or very short	short	short	short	long	short
Premaxilla	enlarged, contact frontals	enlarged, contact frontals	small, no frontal contact	small, no frontal contact	enlarged, nearly contact frontals	small, no frontal contact	small, no frontal contact
Nasals	absent or fused	absent or fused	large	large	small	large, elongate	large
Lacrimal	fused to maxillae laterad of prefrontals or absent; contact orbit	anterior of prefrontals; do not contact orbit	probably laterad of prefrontals; contact orbit	laterad of prefrontals; contact orbit	anterior of prefrontals; do not contact orbit	laterad of prefrontals; contact orbit	laterad of prefrontals, contact orbit
Prefrontals	contact nares	do not contact nares	contact nares	contact nares	do not contact nares	contact nares	contact nares
Orbital position	dorsal, moderately separated	dorsal, close	dorsolateral, separated	dorsolateral, separated	dorsolateral, separated	dorsolateral, moderately separated	dorsolateral, separated
Frontals	long, single	long, single	short, paired	short, paired	short, paired	long, single	short, paired
Prefrontal-Postfrontal contact	no	no	yes	yes	yes	yes	yes, broad

Postorbital	does not touch orbit	does not touch orbit	contacts orbit	contacts orbit	contacts orbit	very narrow contact with orbit	?
Maxilla	does not touch orbit if dorsal part is prefrontal	does not touch orbit	contacts orbit	contacts orbit	contacts orbit	contacts orbit	contacts orbit
Jugal	borders mouth	does not border mouth	<i>ibid.</i>	<i>ibid.</i>	<i>ibid.</i>	<i>ibid.</i>	<i>ibid.</i>
Quadratojugal	no flange; pterygoid contact	flange; no pterygoid contact	no flange;?	no flange;?	possibly flanged;?	no flange;?	no flange
Squamosal	internal flange to quadrate	internal flange to quadrate	internal flange to quadrate	?	internal flange to quadrate	?	?
Length of skull table	long	long	long	long	long	short	long
Width of skull table	very wide	very wide	moderate	moderate	wide	narrow	moderate
Parietals and postparietals	elongated laterally	elongated laterally	narrow	narrow	narrow	very narrow	moderate
Tabular	large, cornuate	large, cornuate	small, cornuate	small, cornuate	moderate, cornuate	small, slightly cornuate	?not cornuate
Otic notch	faces ventrad	faces ventrad	?ventro-posteriad	?	?ventro-posteriad	?	ventro-posteriad
Exocoipital	contacts pterygoid and parasphenoid	contacts pterygoid and parasphenoid	contacts pterygoid and parasphenoid	?	separated from pterygoid and parasphenoid by basisphenoid	?	separated from pterygoid and parasphenoid by basisphenoid

TABLE 3 (Cont.)

CHARACTER	DIPLOCERASPIS	DIPLOCAULUS	DICERATOSAURUS	KERATERPETON	BATRACHIDERPETON	UROCORDYLUS	SCINCOSAURUS
Basioccipital	unossified	?unossified	? small	?	small	?	small
Pterygoid articulation	sutured to parasphenoids	sutured to parasphenoids	sutured to parasphenoids	?	movable, to basisphenoid	movable, to basisphenoid	movable, to basisphenoid
Teeth	small, short	small, short	small, short	small, short	small, short	small, short	?
Marginal tooth row	short	short	short	short	short	long	?
Palatal teeth	arch anterior of the internal nares	arch posterior of the internal nares	double arch, both anterior and posterior of internal nares	?arch anterior of the internal nares	arch posterior of the internal nares, shagreen teeth on pterygoid	?	?
Interpterygoid vacuities	very large	very large	small	?	none	?	small
Quadrate	anterior position	anterior position	slightly anterior	slightly anterior	slightly anterior	posterior	slightly anterior
Epityergoid	braced against skull roof	braced against skull roof	?	?	?	?	?
Mandible form	short, deep, sides subparallel	short, shallow sides diverge	short, deep, sides subparallel	?	short, deep, sides diverge	long, deep, sides subparallel	?
Retroarticular process	present	absent	?	?	absent	?	?
Coronoid process	well developed	low	well developed	?	low	?	?

Articular facets	double, posterodorsal as well as posteromedial	posteromedial	? dorsomedial	? dorsomedial	? ?
Angular	broad lateral exposure	narrow lateral exposure	? ?	narrow lateral exposure	? ?
Splenic	single, not in symphysis, narrow inner flange	double, in symphysis, narrow outer flange	? ?	single, in symphysis, narrow outer flange	? ?
Neural spine form	large, moderately expanded; that of atlas large	large, moderately expanded; none on atlas	large, strongly expanded	? ?	? moderate ?
Neural spine "ornamentation"	small, anastomosing pits and ridges	single large pit	small, circular pits	"Corrugated"	? ?
Neural arch "ornamentation"	none	none	none	? ?	? distal vertical grooves ?
Accessory articulations	zygantra-zygosphene on neural spine	zygantra-zygosphene on neural spine	?zygantra-zygosphene on spine	?zygantra-zygosphene on neural arch	?none zygantra-zygosphene on neural arch
Transverse processes	thoracic double	thoracic double	?single except possibly double on "axis"	? single	? single single

TABLE 3 (Cont.)

CHARACTER	DIPLOCERASPIS	DIPLOCAULUS	DICERATOSAURUS	KERATERPETON	BATRACHIDERPETON	UROCORDYLUS	SCINCOSAURUS
Ribs	double headed	double headed	double in anterior, single in posterior thoracic	double headed in anterior thoracic; not known otherwise	?	double headed	double headed
Centra	fine, vermiculate "ornamentation"	fine, vermiculate "ornamentation"	no ornamentation except possibly on "atlas"	no ornamentation	?	no ornamentation	?
Clavicle	ventral plate triangular, sculptured; dorsal rod slender	<i>ibid.</i>	<i>ibid.</i>	?	more quadrangular	-	?
Interclavicle	pentamerous, sculptured	<i>ibid.</i>	<i>ibid.</i>	?	<i>ibid.</i>	-	?

Rather major functional and adaptive differences presumably underlie this morphological divergence even though the overall pattern is similar.

A flattened body in amphibians correlates, apparently without exception, with a fully aquatic, bottom-living habit. Lateral line canals are also a positive index of aquatic life. The limbs typically are small; fish-like movements of trunk and tail provide the primary means of locomotion. The flattening is associated in some, but not all types, with a bottom-feeding habit; it presumably affords greater stability on the substrate and provides concealment on muddy bottoms or in shallow pools. In some amphibians it is associated with another hallmark of aquatic life, large external gills. In *Diplocaulus* and *Diploceraspis* the massive skull with large horns presumably ballasted the animal and held it to the bottom. The detailed structural adaptations of *Diploceraspis* are imposed upon these general trends.

LOCOMOTION

Although the limbs, the scapula, cleithrum, and coracoid from the shoulder girdle, and the entire pelvic girdle are unknown in *Diploceraspis*, their absence implies small size and incomplete ossification. If functional at all the limbs could not have provided very effective or rapid propulsion. Body and tail movements must have furnished the primary locomotive power.

Among recent vertebrates, accessory vertebral articulations typically indicate extreme flexibility of the spine. Although the movement between individual vertebrae is limited, this limitation provides positive control of movement and permits load distribution along a sinusoid curve. Accessory articulations are well developed in the eel-like neotrideans and imply an eel-like swimming motion. In *Diploceraspis* (and *Diplocaulus* as well) the broad flat body would prevent such an activity, but lateral sinuous motions on the substrate with the legs, the ends of the ribs, and perhaps, the horns, acting as holdfasts would be possible. Romer (1945, p. 159) suggested that up-and-down undulation like that of a skate was possible for *Diplocaulus*. As Douthitt (1917, p. 28) pointed out, however, the zygosphenic articulations would prevent vertical bending movements as would the horizontal zygapophyses and the articulation between the tips of the haemal arches. Since the horns extend far posteriorly of the occipital condyles, vertical movement of the head while on or near the substrate was very limited. Finally the position of the rib heads, one directly above the other, would eliminate vertical movement of the ribs.

On the other hand, the articulation of the ribs with the transverse processes facilitated horizontal movement. The robust ribs may indicate strong intercostal musculature as well as reinforcement of the broad flat trunk. The low vertebral arches imply the shallowness of the long median muscles of the back. The only definite indications of muscle scars on the vertebrae are sharp ridges on the anterior and posterior borders of the transverse processes, a suggestion of strong intertransversarii. Presumably the other segmental muscles of the vertebrae were weak, or, at best, moderately developed.

The low occiput, neural arches, and spines provide very poor angles of insertion for the occipital musculature. The condyles, however, indicate some vertical movement of the head, counterbalanced perhaps by the weight of the horns behind the condyles. The sharp ridge bounding the laterodorsal edges of the occiput probably reflects the insertion of the superficial cervical musculature. The deeper occipital musculature may have inserted broadly over the surface of opisthotic and on the occipital flange of the post-parietal. The lateral bending force of the occipital musculature must have been rather great but since the head could not move laterally on the "atlas," the movement must have been taken up in the trunk.

The caudal vertebrae are strongly compressed in the vertical plane and lack ribs. The tail in consequence was vertically flattened and, by analogy with *Diplocaulus*, very long. The accessory neural spine and haemal arch articulations of the anterior caudals restricted vertical movement; the horizontal zygapophyses would allow extreme lateral bending. The tail, like the trunk, must have moved principally in a sinuous lateral pattern. The slenderness of the tail suggests that it was not the principal driver in locomotion but that it provided a slow glide along the bottom as the animal hunted or fed.

To summarize, the intervertebral articulations and the shallowness of the median epaxial musculature indicates very slight vertical movement though the head could be tilted on the "atlas." The stout transverse processes, the heavy ribs, the position of the rib heads, the intervertebral articulations, and the inferred character of the lateral epaxial and intercostal musculature imply vigorous lateral bending. The limbs, presumably short and weak, the rib ends, and the horns could have served as holdfasts in a sinuous motion along the lake floor. The vertically flattened tail probably supplemented this mode of locomotion and provided a weak but adequate force for a slow glide over the substrate. The

active tail may have also distracted predators from the vulnerable trunk.

FEEDING

The generalized character of the amphibian teeth and jaws as well as the lack of detail on feeding adaptations in Recent forms hinders interpretation of food and feeding habits in fossils. The small, short teeth suggest that the prey was rather small and/or inactive. The sharp, unbroken tips of these teeth argue against food species with heavy shells or carapaces, but the strong basal support of the teeth in the dentary, maxilla, and premaxilla and the bracing of the palatine against the prefrontal suggest that some crushing action was necessary. The relatively broad, short jaws imply a scooping action rather than a direct strike—this also accords with the general clumsy body form and awkward locomotion. The row of palatal teeth just inside and parallel to the marginal row probably assisted with seizure and crushing of small prey. The absence of teeth from the inner areas of the palate again suggests small or inactive prey, for there was apparently no need to hold objects once they were inside the marginal tooth row.

Jaw structure, mechanics, and musculature accord with Watson's generalizations (1951, pp. 53-78) on the flattened amphibians. With the lower border of the mandible resting on the substrate, the skull was tilted up and back to open the mouth. To permit the motion, the jaw articulation was anterior of the occipital condyles. Because the mandible is essentially fixed in position, the depressor mandibulae muscles would pull the occipital border of the skull down and forward and thus assist the occipital musculature in tilting the skull. The considerable development of the retroarticular processes implies that this action was of considerable importance. Their ventrolateral direction implies that the depressors originated from the lateroposterior bones of the otic border. The horns, behind the fulcrum of the occipital condyles, served to counterweight the skull and reduce the muscular effort necessary to tilt it. Since the undersurface of the horns slopes upward behind the quadratojugals, they could move down through perhaps a 12° arc without being forced into the substrate. With the skull tilted back so that the undersurface of the horns lay on the substrate, the mouth would open through a distance slightly greater than the depth of the lower jaw, and produce a gape of four or five millimeters in a large *Diploceraspis*.

The depressor mandibulae muscles, in tilting the skull, placed major stresses on the mandible. The concave arch of the ventral borders of the mandibular rami, the thick ventral portions of the angular and splenial and the complex suture between these elements may have served as adaptations to these stresses.

The jaws were closed, of course, by action of the mandibular adductors which in *Diploceraspis* served to tilt the skull down and forward. Because of the shallowness of the skull, these muscles were limited in length or forced into an unfavorable angle of insertion. The extension of the subtemporal fossae far posterior of the quadrate demonstrates that a large mass, perhaps the greater part, of the adductor system took origin in this area. The quadrate is braced strongly laterodorsally by the quadratojugal, and posterodorsally by the internal flanges of the quadratojugal and squamosal. These supports indicate a strong postero- and laterodorsal pull of adductors, but the absence of direct dorsal bracing implies that few muscle fibers ran directly upward to the under-surface of the jugal. The quadrate is supported mediodorsally by the epipterygoid against the skull roof, medially by the parasphenoid and medioposteriorly by the exoccipitals. This medial bracing provided support against stresses induced by the pterygoid adductors. The lateral facing facet of the quadrate trochlear condyle also indicates a strong median pull.

All of these muscles must have had rather acute angles of insertion on the mandible, particularly those attached to the somewhat elevated coronoid processes. The rugosity near the posterior end of the floor of the adductor fossae suggests that a portion of the posterior adductors inserted by a tendon in this region; the tendon presumably passed over a pulley-like groove on the posterior margin of the fossa. The shallowness and delicacy of the skull forward of the subtemporal fenestra and the lack of a pulley structure along the anterior border of the fenestra imply that the anterior adductors were weak or absent. The mechanical system of the *Diploceraspis* jaw appears to be of the type described by Olson (1961) as "Kinetic Inertial" although the muscle pattern is quite different from other amphibians with this type of jaw action. Adduction of the upper jaw downward onto the lower was rapid, but took its power mostly from the inertia of the moving skull.

The small gape of the mouth, the small teeth, and the marginal position of the palatal teeth coincide in the implication of small prey species. The sharp tips on the teeth argue against a herbivorous habit and suggest rather the necessity of grasping and holding some small active creature. The indication of rapid jaw

action again suggests an elusive prey. The lack of great power in jaw musculature and the delicacy of the teeth would have prevented crushing of heavily armored forms, but the jaws and teeth are sufficiently braced to break up thin valves or carapaces.

RESPIRATION

The nares form the only direct evidence of respiratory structure in *Diploceraspis*, but the body and head form, the probable environment, and the locomotor adaptations suggest respiratory requirements and limit structural possibilities. So far as known, *Diploceraspis* inhabited shallow, warm lakes and ponds (see PALEOECOLOGY). The low oxygen concentration in such environments requires of modern aquatic amphibians: 1) intermittent air breathing, 2) large external gills, or 3) some other specialized mechanism of respiration. In cool, swift water even large forms such as *Cryptobranchus* and *Megalobatrachus* obtain adequate respiration through the buccopharyngeal membranes and the highly vascularized skin (Noble, 1931, p. 468).

The much flattened body of *Diploceraspis* provided a large surface area for gas exchange. Some respiration through the skin seems reasonably probable—the elaborate ornamentation of skull, shoulder girdle, and neural spines may reflect, in some fashion, vascularization of the skin. In view of the large, heavy skull and weak locomotion of *Diploceraspis*, repeated trips to the surface for air seem improbable. In very shallow water, tilting the head up and back would bring the end of the snout to the surface; the position of the nares on the anterior surface of the snout is consistent with such action; but this would only work in an inch or two of water.

Several authors, e.g. Williston (1909) and Douthitt (1917, pp. 31-32), suggested that *Diplocaulus* had external gills and that these were positioned beneath the horns. The same suggestion would presumably hold for *Diploceraspis*. Two separate but related problems enter here: whether external gills were present and what their position might have been. No direct evidence for a branchial system occurs in either *Diplocaulus* or *Diploceraspis*; the gill bars, if present, must have been cartilaginous. The Williston-Douthitt hypothesis then rests on the probable need of these forms for external gills and the presence of such gills in some aquatic amphibians. If present, the gills must have been directed up and out above the horns or down and beneath them. The upper end of the shoulder girdle probably lay very

close to the posterior margin of the skull and, if, as is highly probable, the lateral tips of the opisthotic marked the width of the "neck," there would be no passageway for external gills above the horns.

The shift of the jaw articulation anterior and of the otic area ventroanterior suggests that the pharyngeal region underlay the posterior of the skull. This constitutes a further argument against a dorsal position for the external gills and supports the Williston-Douthitt view. Douthitt recognized that gills in this position would be abraided against the bottom and pointed out that the ventral flange of the *Diplocaulus* quadratojugal formed a protective "pocket." *Diploceraspis* lacks the flange and the pocket; in either form, as the head tilted back to open the mouth, the horns would have forced the gills into the bottom sediment. The arrangement appears quite inefficient if functional at all, and I reject as improbable the suggestion that *Diploceraspis* possessed external gills.

Again, the anterior location of the quadrate, and ventroanterior position of the otic notch suggest that the pharynx lay completely beneath the skull rather than largely posterior to it. The laterodorsal portions of hyobranchial skeleton, so far as developed, should thus have been beneath the otic notches—would, in fact, have supported the ventral wall of the pharynx beneath these notches. The great size and wide extension of the otic notches beneath the horns thus indicate the presence of a pair of very extensive though shallow pharyngobranchial pouches. The precise structure of these pouches is indeterminable. In some Recent larval frogs (Noble, 1931, p. 160) an "opercular" flap covers the branchial area so that the gills on the arches become "internal." In the urodeles the gills are lost prior to the fusion of the operculum to the throat, and the gills are never "internal." In the large form *Cryptobranchus*, a spiracular opening remains after fusion of the operculum; this serves for escape of water brought in during the bucco-pharyngeal respiration.

The pharyngeal pouches of *Diploceraspis* (and *Diplocaulus*) may, therefore, have housed gills (either primarily or secondarily internal) or consisted simply of highly vascularized tissue. The location of the vagus foramina, directed laterally on the ventral surface of the exoccipitals, may reflect the peculiar position of the branchial arches. One cannot determine the nature of the respiratory movements with any probability, but tilting of the head to open the mouth would compress the pharyngeal pouches and expel water. As the head tilted forward to close the mouth

the pouches would expand and draw in water through the nares. The pharyngeal pouches, with or without gills, would greatly increase the respiratory surface, permit survival in low oxygen environments, and protect the respiratory membranes from damage and clogging by the sediment on which the animal moved.

DEFENSE

In many modern amphibians behavior supplements or largely supplants morphological features as protection against predators. In others, poison glands in the skin make the animal unpalatable or even dangerous. The morphologic analysis of defensive mechanisms in fossil forms may miss entirely if such types of protection operated. In *Diploceraspis* certain features of body form appear to be protective, but I cannot claim that this was their primary function or that they were the primary means of defense.

The body shape and habitus of *Diploceraspis* probably concealed the animal against the bottom; one might expect associated adaptations in skin pigment and texture. Since the body was quite flat (a large *Diploceraspis* probably had a trunk-head length of 25 cm., a trunk width of 5 to 7 cm. and a thickness of 2 cm.), attacks would of necessity be made from above, and few potential predators had sufficient mouth gape to pick the animal off the bottom. The head was well protected against dorsal attack by the heavy dermal bone; the neural spines, transverse processes and heavy ribs provided some protection for the trunk. The tail may have distracted enemies from the trunk though the only evidence for this is the relative paucity of caudal vertebrae in the collection.

If, as suggested, the lateral body musculature was powerful, the horns may have served as an effective—even deadly—deterrent. Vigorous contraction of the lateral musculature would have pulled the horns to or even well over the trunk. The pointed and serrate horn tips when driven into the head or gill slits of a shark might well have discouraged further attack. The horns would also prevent a large predator, amphibian or fish, from swallowing even a small *Diploceraspis* whole.

SENSORY ADAPTATIONS

Sensory adaptations in *Diploceraspis* are reasonably obvious. The orbits as in most flattened, bottom animals opened directly upward, and the eyes must have projected above the dorsal surface. Drawn downward into the skull for protection, they probably bulged through the interpterygoid vacuities into the roof

of the mouth. The nares show no special adaptation for olfactory function. The otic capsule is poorly ossified and the stapes is unknown. If the "otic notches" housed pharyngeal pouches (p. 88) and the depressor mandibulae originated on the lateroposterior edges of the notches (p. 85), no room would be left for a tympanic membrane and the "spiracular" opening may have been closed or reduced to a narrow slit. Since any external ear structure would have been pressed against the bottom muds, the need for or value of such a structure is doubtful, and its absence expected *a priori*.

If the otic system was degenerate, the lateral line system was clearly functional. In some Recent newts with optic and olfactory nerves cut, the lateral line organs function as direction and distance perceptors during feeding (Noble, 1931, p. 417). The strong development of the anterior commissure on the premaxillae, the supraorbital canals over the snout, the infraorbital canals across the maxillae and jugals, and the canals of the mandible suggest a similar function in *Diplocaeraspis*. Since the eyes, from their dorsal position, could provide little information on the substrate area ahead of the snout, the lateral line organs may have provided the chief sensory clues in feeding.

THE HORN PROBLEM

Much intellectual effort including my own has been expended on interpretation of the horns of *Diplocaulus* and *Diplocaeraspis*. Williston (1909) and Douthitt (1917, p. 32) suggested that they functioned in *Diplocaulus* to protect the external gills. Douthitt further argued that they counterbalanced the large head but concluded despairingly that head size was itself inadapative and possibly a result of metabolic derangement, as postulated by Case (1911, p. 90). Olson (1951) suggested functions in locomotion and protection.

This peculiar modification of skull presents two separate though related problems. To begin, the horns are *not* excrescences on the posterolateral corners of the skull but are rather extensions of the posterotemporal region. The bones of this region, the parietals, postparietals, tabulars and squamosals accelerated in growth around and above the otic notch so that the notch was enlarged and rolled onto the ventral surface. As growth continued the extreme posterolateral corner of the temporal region accelerated relative to the otic-supraotic region and the tabular portion of "horn" developed. The horn thus comprises three regions: the

proximal infratemporal, the otic, and the distal tabular. I have already ascribed respiratory adaptations to the modified otic area so that in growth at least the horns served initially for support and protection of the pharyngeal pouches. The extension of the infratemporal region (below the squamosal) provided added space for the temporal musculature. The tabular portion of the horn surely served several functions: to counterweight the head, to aid in crawling, to defend the animal against predators, and to ballast and stabilize it on the bottom. The rather marked increase in horn development at the 80 mm. skull length stage in *Diplocaulus* implies that one or all of these functions became critical at about this size and may indicate the time of shift to total bottom living habit. The tabular enlarged at an earlier stage in *Diploceraspis*, but the acceleration of posteriad growth of the horns may have resulted from a comparable functional shift.

The ultimate direction in horn development and function was probably given by three factors:

1. The extreme flattening of the body and skull which reduced the power of cervical and temporal musculature.
2. The necessity of tilting the head to open the mouth.
3. The expansion of the pharyngeal region and the consequent enlargement of the posterior parts of the skull, above the pharynx.

The resultant large, shallow, skull required post-occipital counterweights; the other horn functions are undoubtedly significant but not necessary for existence.³

PRESERVATION AND PALEOECOLOGY

OCCURRENCE

All *Diploceraspis* material has been found in pond or lake deposits defined by massive or laminated gray limestones, clayey limestones, marlstones, and limy shales. Several localities, e.g. 6-55, are lime-pebble or lime-cobble conglomerates. Skull fragments, scales, and teeth of paleoniscids, lungfish, and crossopterygians are typically abundant in the association. Pleuracanthid teeth and spines are also common. Vertebrae of *Lysorophus* and

³Primary adaptive significance is not necessarily of initial phylogenetic significance but may have developed late in the evolutionary history. The presence of tabular horns may in fact have been *sine qua non* for the initiation of the respiratory modifications and the adoption of this particular mode of life. The animal was a functional whole and dissection of different adaptations obscures the totality of a small amphibian highly adapted to the bottom environment of a shallow lake.

Megamolgophis occur at some localities. *Eryops* and other labyrinthodont amphibian material appear at a few places. *Edaphosaurus* is a fairly common associate—at locality 7-55 a partial, articulated skeleton occurred in the same stratum as the abundant *Diploceraspis* specimens. Only one other reptile has been found in a *Diploceraspis* locality (Romer, 1952, p. 105), and even a highly fossiliferous reptile locality like 24-55 has yielded no trace of *Diploceraspis*. Coprolites are common at some localities; these have a characteristic spiral twist, contain bone fragments, and are presumably pleuraecanthid feces.

Diploceraspis skulls are typically broken along a plane of structural weakness near the anterior edge of the parietals, and the horns are commonly separated. Even isolated skull elements from anterior of the break are extraordinarily rare. The halves of the mandible are invariably separated and commonly show additional damage. In spite of breakage, however, the skull fragments preserve delicate structures, including portions of the palate and the horn tips and show no indication of violent rolling or abrasion. The vertebrae are well preserved including the long slender transverse processes, but caudal vertebrae are disproportionately rare. Ribs are extremely rare; clavicles and interclavicles moderately abundant; and pelvic elements and limb bones are not definitely known.

The other vertebrate material occurring with *Diploceraspis* shows similar preservation—entirely disarticulated but with no evidence of abrasion. A wide variety of sizes and shapes occurs on the same bedding surface with no clear evidence of sorting. In some cases, individual beds consist predominately of bone; the internal cavities of most *Diploceraspis* skulls are filled with fish scales and teeth.

ENVIRONMENT OF PRESERVATION

The vertebrate associations, fish and aquatic amphibians, and the lithology indicate burial in lakes and ponds. The elastic lime beds appear to be desiccation conglomerates. No clear evidence exists for strong wave or current action; the lack of abrasion and the preservation of delicate structures indicate otherwise. Warm temperatures and abundant algae presumably account for the deposition of calcium carbonate. Burrowing organisms—except possibly for the lysorophids—are unknown, but the irregular distribution of the fossils, across as well as on the depositional surfaces, implies some reworking.

If wave or current action was not responsible for disarticulation and fragmentation of the *Diploceraspis*, then predators and/or scavengers must have broken and dragged the bodies apart. Horns are obviously inedible and dangerous to an animal that swallowed them. The vertebrae are equally inedible and the shallowness of the back musculature and the prominent neural and transverse spines would make the trunk vertebrae unattractive to all but small scavengers. The tail, however, somewhat less "bony" and well muscled, would probably provide a meal for a moderate sized shark or even an *Eryops*. The lateral trunk area, the limbs, and the face would be equally appetizing. In all, the preservation suggests scavenging or predation by a form capable of breaking and swallowing the small bones, and sufficiently small to reject vertebrae and horns. The pleuracanthid sharks are obvious candidates; *Diploceraspis* bone fragments occur in what appear to be pleuracanthid coprolites. Smaller scavengers cleaned the flesh from vertebrae and skull. The filling of scales in skull cavities demonstrates that the flesh had been removed before burial.

Most *Diploceraspis* localities produce only a few specimens. These presumably represent the typical environments of life and burial: sedimentation rather rapid, population sparse to dense, mortality low to moderate, and environment of preservation unfavorable. A few localities, the bone beds, present special problems. The abundance of fossils here implies action by one or all of four factors: slow sedimentation, dense population, catastrophic mortality, and a favorable environment for preservation. Most of these bone concentrations occur at the transition from limestone to laminated limy shale. The transition itself implies changes in rate of sedimentation, kind of sedimentation, and/or in pH. Any one of these changes might have induced temporary, slow sedimentation or a population increase or catastrophic mortality or a favorable environment of preservation. The data at hand do not provide a unique solution.

LIFE ENVIRONMENT

The evidence cited above indicates that the present occurrence of *Diploceraspis* corresponds with the life environment. Although burrowing organisms may have mixed the vertebrates, it seems likely that the faunal associations represent a biocoenosis. The physical environment then was lacustrine and warm. The association of a swamp-lake border herbivore, *Edaphosaurus*, suggests shallow water, but the presence of sharks and fish several feet in

length demonstrates depths of several feet, at least during high water. The lysorophids and lungfish from the Texas Permian occur in seasonal ponds with evidence of aestivation; their presence here suggests seasonally stagnate, warm and turbid environments.

Diploceraspis is not known from river channel deposits, from floodplain claystones nor from non-carbonate lacustrine shales and siltstones. These lithologies have been searched with some determination but little success: a small reptile skeleton, a *Megamolgophis* vertebra, several *Edaphosaurus* fragments, an eryopsid intercentrum, and perhaps a dozen pleuracanthid teeth. The absence of *Diploceraspis* might well be an accident since the total collection is so small and these lithologies are extremely difficult to search in road cut outcrops. The implication remains, however, that *Diploceraspis* was largely limited to marly lakes and ponds, although one can only speculate on the limiting factors.

Probable predators include the pleuracanthid sharks, *Eryops*, crossopterygians, and for small individuals, *Megamolgophis* and some of the paleoniscids. Selective preservation limits knowledge of potential food species. Ostracods, small gastropods, *Spirorbis*, and estherids are locally abundant and would be "bite-size" for *Diploceraspis*. Since the accumulation of specimens in the *Diploceraspis* bone beds may represent a number of years mortality—or a few minutes—estimates of population density are meaningless. The rarity of small individuals, even fragments, implies low mortality rates after the larval period, but differential preservation may have altered relative abundance significantly.

PHYLOGENY AND EVOLUTIONARY PATTERN

INTRODUCTION

The lack of information on function and adaptation among keraterpetontids as well as the incomplete record hinders interpretation of phylogeny and evolution. Small scale similarities and differences in skulls and vertebrae may represent stable characters evolved early in the radiation of the group and thus may serve to unite genera in phyletic lines and to distinguish between parallel lineages. Or they may represent adaptive parallels and divergences developed late in the evolutionary history of the various lineages.

The time sequence is also somewhat troublesome. *Batrachiderpeton* occurs near the base of the Westphalian series; *Keraterpeton* in slightly higher beds, and *Diceratosaurus* at the top of

the series. *Diplocaulus* appears in lower Stephanian rocks; *Diploceraspis* near the middle of the Stephanian series. If both long-horned forms derived from *Diceratosaurus*, the transformation of skull occurred in a remarkably short period of time. If they evolved from *Batrachiderpeton* or a contemporary, they left no record for the remainder of the Westphalian.

RELATIONSHIP OF *Diploceraspis burkei* AND *D. conemaughensis*

Romer (1952, p. 73), comparing very limited suites of the Conemaugh and Dunkard *Diploceraspis*, concluded that they probably represented distinct species and named them, respectively, *D. conemaughensis* and *D. burkei*. He stated that *D. conemaughensis* differed from *D. burkei* "by smaller size, somewhat lesser 'horn' attenuation, and a lesser degree of curvature and spinescence at the 'horn' tip." He also suggested that the punctate sculpture was finer. No additional *D. conemaughensis* have been found, but the extensive suite of *D. burkei* specimens makes further comparison desirable.

All *D. conemaughensis* specimens are smaller than the largest *D. burkei*; one is smaller than any *D. burkei* yet collected. With the exception of this very small individual, however, the *D. conemaughensis* lie within the size range of *D. burkei*. Because of the lack of a definite adult stage and the small number in the *D. conemaughensis* sample, one cannot now conclude that *D. conemaughensis* averaged smaller in size.

The degree of horn attenuation in *Diploceraspis burkei* increases with total size and also varies considerably among individuals of similar size. The apparent stubbiness of the horn in *D. conemaughensis*, therefore, reflects the size of specimens rather than implying specific difference. Curvature and spinescence of the horn tips vary considerably between individuals of *D. burkei* and may also increase with size. The pitting of external bone is also in the *D. burkei* size range. These characters cannot serve to define *D. conemaughensis*.

The apparent size difference may be real. Certainly, the difference in age, mid-Stephanian against very late Stephanian-early Autunian would imply the existence of morphologically distinct groups. Consequently, I believe it best to retain the name of *D. conemaughensis* with the recognition that additional collecting may show it to be a synonym of *D. burkei*.

Romer pointed out that *D. conemaughensis* indicates precocious development of the horns in this lineage. If the *D. conemaughensis* specimens represent a population of relatively small individuals,

the other known differences represent allometric development in the larger individuals of *D. burkei*. By this token, *D. conemaughensis* represents the ancestral population for *D. burkei* or is so close to it as to make no difference.

RELATIONSHIP OF *Diploceraspis* AND *Diplocaulus*

Romer (1952, pp. 67-72) emphasized that *Diploceraspis* differed from *Diplocaulus* in spite of their superficial similarity and argued that they represented distinct though parallel evolutionary lines. Although the current study demonstrates additional similarities, it also shows marked dissimilarities between the two genera. In general, the similarities (other than the basic neotridian pattern) concern flattening of the skull and body and development of horns. These include:

1. Dorsal position of orbits.
2. Loss of prefrontal-postfrontal contact.
3. Separation of maxilla from border of orbit.
4. Lateral expansion of squamosal, tabular, parietal and post-parietal.
5. Ventral position of otic notch.
6. Loss of basisphenoid and basioccipital.
7. Development of large interpterygoid vacuities.
8. Sutural junctions of pterygoid to exoccipital and parasphenoid and of latter to exoccipital.
9. Anterior position of quadrate.
10. Brace of pterygoid against parietal by epipterygoid.
11. Presence of long, double, transverse processes on vertebrae.

Most of these characteristics developed in other amphibian evolutionary lineages with flattening of the skull; they indicate little about phylogeny.

The reduction (or fusion) of the nasals, the fusion of the frontals and the shift of the postorbital away from the orbital border in *Diploceraspis* and *Diplocaulus* may also relate to change in skull shape though the adaptive significance is not apparent. The vermiculate pattern on the centra similarly lacks apparent functional importance. These three characteristics, therefore, are the only "non-adaptive" or "conservative" characteristics that cannot be found in the other keraterpetontids.

The apparent adaptive differences between the two genera lie primarily in these characteristics of the jaws and teeth in *Diploceraspis*:

1. The presence of the jugal on the border of the mouth.

2. The absence of a ventral flange on the quadratojugal.
3. The arch of palatal teeth anterior of the internal nares.
4. The relatively greater size of the teeth.
5. The greater depth of the mandible and the presence of a coronoid process.
6. The presence of a retroarticular process.
7. The dorsal direction of the articular facets.
8. The wide lateral exposure of the angular.
9. The single splenial with wide lateral and narrow medial flanges.

The differences in the snout, i.e. the position of the lacrimals laterad of the prefrontals and nasal contact of the prefrontals in *Diploceraspis*, lack apparent adaptive meaning as do the large neural spine on the "atlas," the fine pitting on the neural spines, the contact of the quadratojugal with the pterygoid, and the exclusion of the squamosal from the otic notch. These at least counterbalance the "nonadaptive" similarities cited; since they occur in spite of overall parallelism in adaptation, they probably have greater significance.

Finally, the development of the horns apparently differs radically in *Diploceraspis* and *Diplocaulus*. As described in a preceding section, the horn of *Diploceraspis* shows a strong laterad growth gradient in early development succeeded by a strong posteriad gradient; horn development in *Diplocaulus* begins with posteriad extension and concludes with laterad.

I conclude from this analysis that the two "long-horned" neotrideans evolved their horns in parallel from a common "short-horned" or hornless ancestor. The great similarity of the two implies common ancestry; the difference in details of skull and vertebrae and in the form of teeth and jaws indicates a period of separate evolution prior to their appearance. The difference in development of horns suggests that the two lineages separated prior to the evolution of elongate horns.

PHYLOGENY OF THE KERATERPETONTIDS

The keraterpetontids (summary in Table 3), taken in the broad sense, comprise three rather distinct morphologic groups. The oldest, and in many ways the most primitive group, includes *Batrachiderpeton*. This form, in spite of the relatively large horns, shows primitive characters in palate and basicranium. No interpterygoid vacuities are present; the pterygoid articulation with the basicranium is movable; the basisphenoid and basiptyergoid

are well ossified; and the exoccipital lacks pterygoid and parasphenoid contacts. The jaw articulations lie in line with the occipital condyles.

The group also includes *Scincosaurus*. Its morphology and relationships are not well known, but it, alone among the keraterpetontids, appears to lack horns. As in *Batrachiderpeton*, the

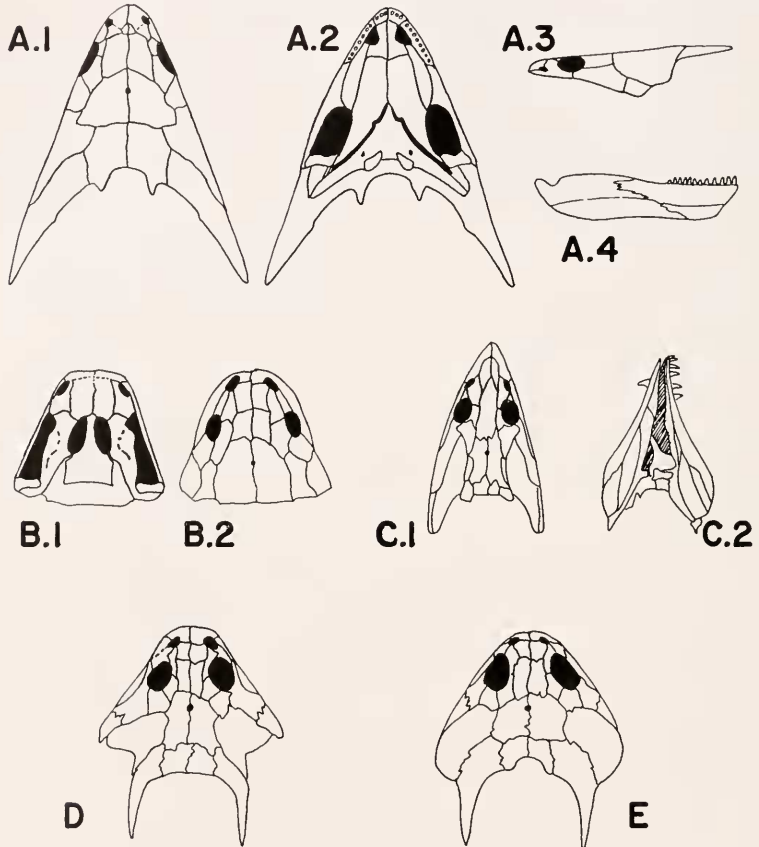


FIG. 12. The neotridean skull. *A*, *Batrachiderpeton*, after Watson, 1913. *A.1*, Dorsal reconstruction, approximately $\times 0.5$. *A.2*, Palatal reconstruction, approximately $\times 0.5$. *A.3*, Lateral view, approximately $\times 0.4$. *A.4*, Mandible, approximately $\times 0.8$. *B*, *Scincosaurus*, approximately $\times 2.4$, after Steen, 1938. *B.1*, Palatal reconstruction; *B.2*, dorsal reconstruction. *C*, *Urocordylus*, approximately $\times 0.45$, after Steen, 1938. *C.1*, Dorsal reconstruction; *C.2*, ventral view. *D*, *Keraterpeton*, dorsal reconstruction, approximately $\times 0.8$, after Steen, 1938. *E*, *Diceratosaurus*, AMNH 6856, dorsal view, approximately $\times 0.8$.

basisphenoid and basiptyergoid are well ossified; the exoccipital is limited to the posterior border of the skull, and the pterygoid has a movable contact with the basicranium. Small interptyergoid vacuities are present, however, and the jaw articulations lie slightly ahead of the condyles.

Keraterpeton and *Diceratosaurus* form a second group marked by short horns, a reduced basicranium (basisphenoid and basioccipital), sutural junctures between pterygoid, parasphenoid, and exoccipital, and moderately large interptyergoid vacuities. The

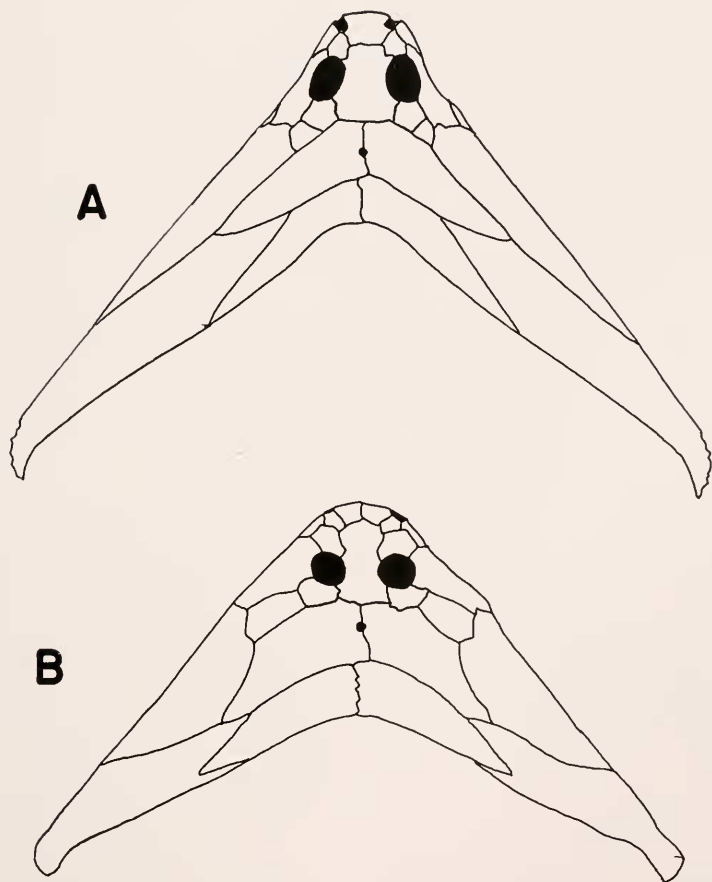


FIG. 13. The neotridean skull. A, *Diploceraspis*, dorsal reconstruction, approximately $\times 0.5$. B, *Diplocaulus*, dorsal view, Chicago Natural History Museum CNHM-UC 636, approximately $\times 0.25$, after Olson, 1951.

jaw articulation is some distance in front of the condyles. They differ significantly only in ornamentation of the neural spines and in excavation of the posterior border of the postparietals near the median line in *Diceratosaurus*.

Diplocaulus and *Diploceraspis* make up a third group. They differ from those in the second by extreme development of the horns, by a further anterior shift of the articulars, by the extreme flattening of the skull, and by the great size of interpterygoid vacuities. The differences between the two genera were discussed in the preceding section.

These morphologic grades are not necessarily evolutionary or taxonomic units. The evidence is against the unity of the third group, and the phyletic lineages probably crosscut all groups. *Scincosaurus* occupies an isolated position. Though it might have been derived from *Batrachiderpeton* by reversal of the trend in horn evolution, the only positive evidence is to the contrary. The arrangement of snout elements in *Scincosaurus*, i.e., the lateral position of the lacrimal and its contact with the orbit, represents the primitive neotridean condition. The arrangement in *Batrachiderpeton* of the lacrimal anterior of the prefrontal and excluded from the orbit occurs only in *Diplocaulus* among the other neotrideans. *Scincosaurus* retains the primitive basieranian-palatal characteristics lost in the *Keraterpeton* group and so cannot have been derived from there. It is too late in time to be the ancestor of *Keraterpeton*, although it may represent a conservative lineage retaining some of the characters of that ancestor.

Batrachiderpeton, in palate and basieranium, would form an ideal ancestor for the remaining keraterpetontids. Although the horns are slightly larger and diverge more than those of *Keraterpeton* and *Diceratosaurus*, this would not seem to disqualify them as ancestors. The arrangement of bones in the snout is troublesome, however. Evolution would, necessarily, have had to reverse the modified (?specialized) position of the lacrimal in *Batrachiderpeton*. On the other hand, this character connects *Batrachiderpeton* to *Diplocaulus*. The two also resemble each other and differ from the *Keraterpeton* group and *Diploceraspis* in the lack of a coronoid process on the mandible and in the arch of the vomerine teeth posterior of the internal nares. Watson suggested (1913) that *Diplocaulus* evolved from *Batrachiderpeton*, and I see nothing in the current comparisons to contradict his conclusion.

Keraterpeton and *Diceratosaurus* are nearly contemporaneous in middle and late Westphalian time. Their differences, so far as

known, are comparable to those in closely related contemporaneous genera (and therefore slightly divergent lineages) or to successive genera in a single lineage. No decision seems possible on present evidence. Their ancestry must be in a population similar to the early Westphalian *Batrachiderpeton* but distinguished

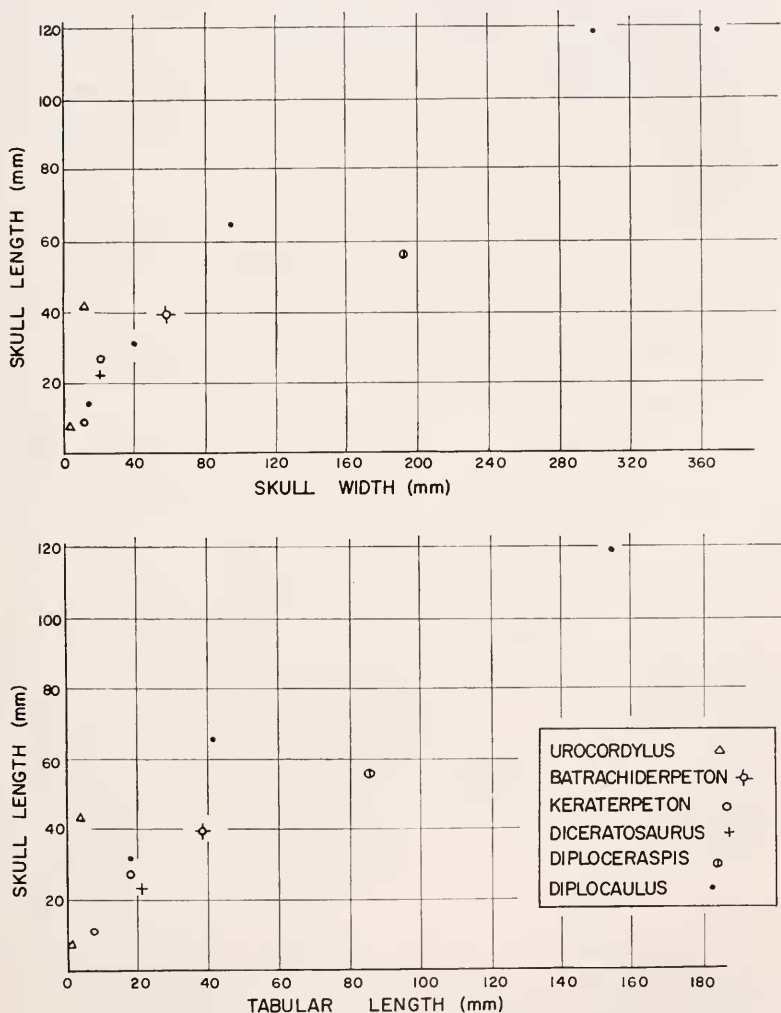


FIG. 14. Nectridean skull proportions. Upper graph shows skull length plotted against skull width; lower graph shows skull length against tabular length. See Table 2 for definition of measurements.

by retention of the primitive position of the lacrimal.

Diploceraspis, as demonstrated above, parallels *Diplocaulus* rather than lying in or near its lineage. As *Diplocaulus* and *Batrachiderpeton* are united by character of snout, supplemented by similarities in jaw and palatal tooth row, so *Diploceraspis* and *Diceratosaurus* are also united. They share the primitive lateral position of the lacrimal. The palatal tooth row of *Diceratosaurus* is double, but the principal series, like that of *Diploceraspis*, curves anteriorly of the internal nares. The two have similar high coronoid processes. Finally, the sculpture of the neural spines is very similar. I concur then with Romer (1952, pp. 71-72) that *Diploceraspis* evolved from a *Diceratosaurus* population.

Figure 15 summarizes the phyletic scheme just discussed. As reconstructed, it includes eight distinct morphologic-phyletic units (three lineages and four grades of morphologic specialization) only five of which are known from fossils. Only one of these units comprises as many as two genera although a wider knowledge of Carboniferous amphibians would probably fill out some of the

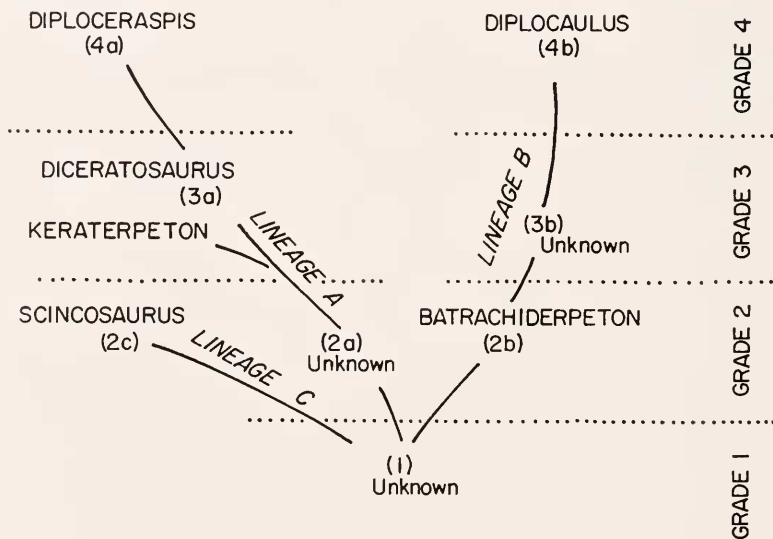


FIG. 15. Phylogeny of the keraterpetontids. Note that three genera postulated in interpretation are not known from the fossil record. The stratigraphic sequence of forms in Lineages A and B accords with the inferred phylogenetic sequence. The "grades" are morphological levels indicating the approach to the specialized condition in *Diploceraspis* and *Diplocaulus*.

groups. The taxonomic arrangement should reflect this phyletic pattern, but several alternatives exist.

Romer (1945, p. 591) includes the horned genera then known, as well as *Scinosaurus*, in a single family, the Keraterpetontidae. Logically, *Diploceraspis* would fall here also. Although some paleontologists (e.g. Case, 1946, p. 351) regard *Diplocaulus* as sufficiently distinct to be placed in a separate family, this would require recognition of a superfamily with at least two and possibly four families for the five well known genera. If *Batrachiderpeton* is placed with *Diplocaulus* in this separate family as it has been by many workers (e.g. Case, 1946, p. 351), the vertical splitting of lineages would approach absurdity. *Batrachiderpeton* differs from the probable ancestor of *Diceratosaurus* (Unit 2a in Fig. 15) by only a single character, the position of the lacrimal, hardly more than a specific difference in a tightly knit genus. But the suggested arrangement would set it in a separate family.

All in all, I believe it best to retain the taxonomic scale suggested by Romer, to regard these six genera as members of a single family and to use subfamilial ranks to indicate phylogeny. Again, extreme vertical or horizontal classifications are possible, but the most reasonable compromise seems to be the recognition of a "primitive" horizontal subfamily, *Batrachiderpetontinae*, which would include the hypothetical ancestors of the entire family (Unit 1), *Batrachiderpeton* (Unit 2b), the postulated ancestor of *Diceratosaurus* (Unit 2a), and *Scinosaurus* as *incertae sedis*. A vertical subfamily, *Keraterpetontinae* would include *Diploceraspis* (4a) as well as *Diceratosaurus* and *Keraterpeton* (3a). A second vertical subfamily, *Diplocaulinae*, would be formed for *Diplocaulus* (4b) and the as yet undiscovered genus (3b) linking it to *Batrachiderpeton*. The arrangement of subfamilies and their diagnostic characteristics would be:

Family Keraterpetontidae Romer 1945

Nectrideans with slightly or strongly flattened skull, tabular "horns," short snout, jaw articulation anterior of occipital condyles, short tooth row, and some type of accessory articulations between vertebrae.

Subfamily *Batrachiderpetontinae*

Skull moderately flattened; horns absent, short, or of moderate length; jaw articulation about on line with or just ahead of condyles; paired frontals; interpterygoid vacuities small or absent; basioccipital and basisphenoid ossified; movable pterygoid-basisphenoid articulation;

no sutural contact between exoccipitals, pterygoids, and parasphenoids.

Batrachiderpeton, ? *Scincosaurus*.

Subfamily Keraterpetontinae.

Skull moderately to strongly flattened; horns short to long; jaw articulation far anterior of condyles; interpterygoid vacuities moderate to large; frontal paired or single; basioccipital and basisphenoid reduced or unossified; sutural junction of pterygoid with parasphenoid; sutural junctions of exoccipital with pterygoid and parasphenoid; lacrimal laterad of prefrontal and bordering orbit; arch of vomerine teeth anterior of internal nares; well developed coronoid process; neural spines of vertebrae pitted or corrugated.

Keraterpeton, *Diceratosaurus*, *Diploceraspis*.

Subfamily Diplocaulinae

Skull moderately to strongly flattened; horns short to long; jaw articulation far anterior of condyles; interpterygoid vacuities moderate to large; frontal paired or single; basioccipital and basisphenoid reduced or unossified; sutural junction of pterygoid with parasphenoid; sutural junctions of exoccipital with pterygoid and parasphenoid; lacrimal anterior of prefrontal and separated from orbit; arch of vomerine teeth posterior of internal nares; coronoid process absent from mandible; neural spines smooth except for single large pit.

Diplocaulus.

ADAPTATION AND EVOLUTION OF *DIPLOCERASPIS*

Watson (1951, pp. 41-49, 66-76, 89-90) described the typical evolutionary sequence in the flattening of the amphibian skull and discussed the adaptive significance of this change. Among the labyrinthodonts, the modification is associated with a fully aquatic habit, but even the brachyopids which most resemble *Diploceraspis* are much larger and presumably fed on moderate sized vertebrates as do crocodiles now. In the latter the flattened form is an adaptation to concealment and locomotion in shallow water not for bottom feeding.

The morphology of *Diploceraspis* and *Diplocaulus* strongly suggests bottom-feeding adaptations and thus the parallel with the labyrinthodonts is primarily structural not functional. In this circumstance, some morphologic divergence, i.e. the development

of horns, the rotation of the pharyngeal region, the extreme anterior position of the jaw articulation, and the strength of vertebrae and ribs, is to be expected. Preceding sections of this paper describe the functional importance of these characteristics; their evolutionary origin requires explanation.

The character and proportions of snout, jaws, and teeth remain similar (Table 3) in all keraterpetontids. The *Batrachiderpeton-Diplocaulus* lineage has more extensive development of teeth on the inner portions of the palate, and these animals may have taken larger and/or more active prey, e.g. large worms, that could not be engulfed in a single bite. If this interpretation is correct, the initial divergence of the two lineages would be related to differences in feeding between two otherwise similar populations.

The structure of the primitive keraterpetontids implies more active locomotion than that of *Diploceraspis* and *Diplocaulus*, and these forms may have sought food above the bottom, at the surface, or even on land. The incipient flattening of skull and body suggests, however, that the bottom-feeding habit was already primary.

Batrachiderpeton shows slight differentiation of tabular and supratharyngeal portions of the horns; in *Diceratosaurus* the difference is marked and the ventrad rotation of the otic surface has begun. The tabular horns of these early keraterpetontids may have had some function in defense though their position proximal to the upper end of the cleithrum must have limited their mobility and usefulness. Since the pharynx lay largely behind rather than beneath the skull roof, they may have served a largely passive function in support and protection of the pharyngeal region, in particular of an opercular flap.

The throat and shoulder region of the primitive genera provide sufficient space for egress of external gills though no branchial arches have been observed. The coal swamp and pond deposits from which these forms come probably had low partial oxygen pressures and external gills would be useful though perhaps not necessary. The development of the supratharyngeal horn in *Diceratosaurus* indicates some development of pharyngeal pouches leading on to *Diploceraspis*. The parallel development of these pouches in *Diplocaulus* would tend to demonstrate an antecedent structure in their common ancestor — possibly external gills plus a protective flap, internal gills in pharyngeal pouches, or simply vascularized pharyngeal pouches. Present morphological evidence does not discriminate between these alternatives.

The changes between the short- and long-horned types represent completion of the adaptation to bottom feeding in shallow ponds. The trends of flattening, horn development, modification of the palate, and shift of the jaw articulation were carried to their adaptive extremes. Whatever the function of the horn in the primitive forms, its further modification is related to a complex of apparently inseparable functions. The supratharyngeal portion enlarged to cover and support the pharyngeal pouches, but this enlargement was functionally possible only if the tabular portion extended to counterbalance the added weight. The total weight of skull was valuable in holding the animal on the substrate but was tolerable in locomotion only if the animal remained on the bottom. Continuous bottom life was possible only to an animal with a modified respiratory system, i.e. with pharyngeal pouches. The horns counter-weighted the skull in opening the mouth, but because they limited the amount of tilting and thus the mouth gape, only animals that ate small organisms would be viable.

The initial feeding adaptations in teeth, jaw and snout, therefore, preconditioned the evolutionary history of the keraterpetonids. Whether the horn structure was pre-adaptive remains uncertain; the presence of the horn, however, was necessary for the particular evolutionary path that developed. If *Diceratosaurus* is the direct ancestor of *Diploceaspsis*, the evolutionary shift was rapid — between the late Westphalian and middle Stephanian — but nearly all the unique structural features of *Diploceaspsis* are foreshadowed in *Diceratosaurus* and might involve a very few genetic changes as these affected growth gradients and fields.

SUMMARY

New specimens of the nectridean amphibian, *Diploceaspsis*, from the Dunkard group, late Pennsylvanian-early Permian of Ohio, Pennsylvania, and West Virginia, provide additional morphologic information. The skull is broad and flat with a short snout, upward facing eyes, elongate tabular horns, and ornamentation of closely spaced circular pits. The jaw articulation lies far forward of the occipital surface. The basiscanium is reduced, and extensive sutures join the pterygoid, parasphenoid, and exoccipital. The vertebrae are characterized by sculptured centra and neural processes. The ribs are long, straight, and double-headed. The clavicles comprise a triangular, sculptured ventral plate and a slender, rod-like ascending process. The interclavicle is relatively large, pentamerous, and sculptured. The trunk, like

the skull, is broad and flat; the tail is slender and compressed in the vertical plane. *Diploceraspis* shows major similarities to *Diplocaulus* as well as significant minor differences. The features of these two "long-horned" forms are anticipated in varying degrees by the earlier "short-horned" neotridians, the keraterpetontids.

The form and occurrence of *Diploceraspis* indicate a shallow lacustrine habitat. They crawled on the bottom and were probably very weak swimmers. They fed on small invertebrates collected from the substrate. The enlarged otic area presumably covered large pharyngeal pouches that served for respiration in low oxygen environments. The horns counterbalanced the weight of the skull over the condyles, ballasted the animals to the bottom, supported and shielded the pharyngeal pouches, and assisted in defense.

Diploceraspis evolved in parallel to *Diplocaulus*. *Diceratosaurus* is the probable ancestor of the former, *Batrachiderpeton* of the latter. The common ancestor of these horned amphibians was slightly antecedent to and little different from *Batrachiderpeton*. The early keraterpetontids were probably active swimmers and possibly partly terrestrial; the "long-horned" types evolved in adaptation to a completely aquatic, bottom-feeding life with its stringencies and possibilities.

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